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Seattle, Washington

U.S. DEPARTMENT OF COMMERCE
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NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

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SCIENTIFIC EDITOR, *Fishery Bulletin*

Dr. Andrew E. Dizon
Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, CA 92038

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AWARDS

The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by the NMFS scientists and published in the *Fishery Bulletin* for 1986 and the *Marine Fisheries Review* for 1985. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following papers were judged as the best in meeting this requirement.

***Fishery Bulletin* 1986 — Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods, by Gail M. Theilacker. Fish. Bull., U.S. 84: 1-17. Gail M. Theilacker is with the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA.**

***Marine Fisheries Review* 1985 — Biology of the red sea urchin, *Strongylocentrotus franciscanus*, and its fishery in California, by Susumu Kato and Stephen C. Schroeter. Mar. Fish. Rev. 47(3):1-20. Susumu Kato is with the Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA, and Stephen C. Schroeter is with the Department of Biological Sciences, University of California, University Park, CA.**

INTERANNUAL VARIATION OF ICHTHYOPLANKTON COMPOSITION AND ABUNDANCE RELATIONS OFF NORTHERN CHILE, 1964–83

VALERIE J. LOEB[1] AND OMAR ROJAS[2]

ABSTRACT

Larval fishes were collected off of northern Chile during winter (July–September) ichthyoplankton surveys undertaken in 1964–70, 1972–73, and 1983. The 19-year timespan included a wide variety of hydrographic conditions in the Humboldt Current area (cold years, El Niño events, and intervening transition years); it also included the decline and collapse of the anchoveta fisheries and increases of sardine, mackerel, and jack mackerel stocks off northern Chile and Peru. The ichthyoplankton data are examined in relation to ambient hydrographic conditions as well as to possible chronological changes in environmental conditions which led to the increased Chilean sardine stocks and anchoveta fishery collapse.

More coherent patterns come from considerations of larval fish species composition in 1964–69 and 1970–73 data sets than from years of "similar" hydrographic conditions. A marked shift in relative abundances of nonfished mesopelagic species in 1969–70 is associated with changes within long-term physical data bases from Chile and Peru suggesting a large-scale environmental change. Sardine stock growth began with successful larval survival of 1968–69 and later year classes. Anchoveta stock decline began in 1972 probably due to poor larval survival. Affiliation of anchoveta and coastal species larval abundance implies that they are similarly influenced by coastal processes. An atmospherically driven oceanic circulation change beginning in the late 1960's and possibly involving onshore presence of subtropical and/or oceanic waters and altered coastal processes may have been responsible for the changes in the northern Chilean fish assemblages.

The Humboldt Current region, like the other major eastern boundary current systems (California, Benguela, and Canary Currents) is dominated by pelagic schooling fish stocks including anchoveta (*Engraulis*), sardine (*Sardinops*), hake (*Merluccius*), mackerel (*Scomber*), jack mackerel (*Trachurus*), and bonita (*Sarda*) (Parrish et al. 1983). These fish stocks, like those in the other eastern boundary current areas, exhibit extreme population fluctuations. Most notable in the past 30 years are the collapses of Peruvian and Chilean anchoveta stocks in the mid-1970's and their succession by sardine and, to a lesser extent, mackerel and jack mackerel stocks (Santander and Flores 1983; Serra 1983).

Hydrographic complexity and variability are characteristic of eastern boundary current systems. Included in the Humboldt Current region are equatorial, subequatorial, subantarctic, and antarctic oceanic water masses; northward flowing currents and opposing countercurrents; and wind driven, seasonally variable coastal upwelling (Wyrtki 1967). Additionally, the region is subject to 1) large seasonal and longer period fluctuations in advection of water masses of markedly different properties and 2) large interannual differences in the timing and intensity of seasonal upwelling processes (Bakun 1987; Bernal et al. 1983; Parrish et al. 1983; Robles et al. 1976). The clearest and generally considered most important of the nonseasonal processes influencing the biology of the current system is the El Niño phenomenon (Bernal et al. 1983; Guillén 1983). El Niño events off Peru and Chile are marked by large-scale atmospherically driven southward and coastward advection of warm, high-salinity equatorial and subequatorial surface waters, weakening of coastal upwelling (or upwelling of warm nutrient-poor waters), and weakening of subsequent phytoplankton blooms. These El Niño or warm-water periods are variable in their intensity and duration (Guillén 1983; Santander and Flores 1983). In contrast to these periods are more "normal" cold-water events resulting from atmospherically driven intensification of northward flowing cold, low-salinity subantarctic waters and seasonal upwelling of cold, nutrient-rich water. Major El Niño events occurred in 1891, 1925–26, 1940–41, 1957–58, 1965, 1972–73, 1976, and 1982–83;

[1]Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, CA 95039.
[2]Instituto de Fomento Pesquero, Avenida Pedro de Valdivia 2633, Casilla 1287, Santiago, Chile.

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major cold events over the past 20 years occurred in 1964, 1967–68, 1970–71, and 1974–75 (Guillén 1983).

The decline and ultimate collapse of the anchoveta fisheries of Peru began in 1970 and was finalized by the intense 1972–73 El Niño; the northern Chilean stock decline started in 1972 and was finalized by 1977. Factors facilitating these declines are generally believed to include overfishing and the devastating effects of the El Niño on anchoveta spawning behavior and intensity as well as on subsequent recruitment. Competition and/or predation pressure resulting from increasing abundances and distributions of sardine and mackerel have also been hypothesized (Santander and Flores 1983; Serra 1983).

Because of the great socioeconomic value of the dominant pelagic fish species of the Peru-Chile ecosystem, their population fluctuations have received a great deal of attention over the past 20 years. However, coincidental changes in the composition, abundance, or spawning intensities of other commercially less important and nonharvested species have not been examined. Information on the changes of these unfished species in relation to hydrographic conditions and fluctuations of the dominant pelagic fish stocks provide additional insight into the ecology of the Humboldt Current and may elucidate possible causes for the dramatic changes which occurred during the 1970's.

In the present work we examine the abundance and composition of total ichthyoplankton assemblages collected off of northern Chile (lat. 18°-24°S) during 1964–73 and 1983 in relation to ambient hydrographic conditions. "Normal" cold water as well as warm-water and El Niño events occurred during the 19-yr sampling span. We also examine our results with respect to possible chronological change in environmental conditions which led to the 1977 anchoveta fishery collapse off northern Chile. Our results may be applicable for interpreting coincidental changes in the Peruvian ecosystem and may also be broadly applicable for studies of similar changes in the other eastern boundary current ecosystems.

METHODS

Samples were collected during 1964–73 and 1983 ichthyoplankton surveys conducted by the Instituto de Fomento Pesquero. The area most intensively surveyed was a narrow coastal strip extending between Arica and Antofagasta (lat. 18°-24°S, long. 70°-72°W; Fig. 1). This area includes one of two major anchoveta (*Engraulis ringens*) spawning grounds off Chile and the primary sardine (*Sardinops sagax*) spawning area off Chile prior to 1973 (Fig. 2A, B). All samples used for interannual comparisons were collected during late July–September following peak winter anchoveta and sardine spawning periods. Between 21 and 87 samples from the 18°–24°S area were analyzed for each of 11 cruises (Table 1). In one case data from two cruises (August and September 1968) were pooled to provide adequate coverage. Sampling was done annually from 1964 to 1970 and in 1972 and 1973. There was a 10-yr hiatus before regular sampling was resumed in 1983.

The 1964–73 samples were collected with Hensen nets (0.28 m^2 mouth opening; 300 μm mesh). Prior to 1973 the vertical net hauls were 50–0 m; in 1973 haul depth was increased to 100 m. The 1983 100–0 m vertical hauls were made with WP2 nets (0.25 m^2 mouth opening; UNESCO 1968) of 300 μm mesh. Samples were preserved using buffered 5% formalin solution. Sea surface temperature and salinity data were collected at most sampling stations for all but two winter cruises; these data are lacking for 1970 and salinity data are minimal for 1967.

All fish eggs and larvae were removed from samples, and invertebrate zooplankton biomass was measured. Wet weight displacement volume was measured for 1964–73 samples; in 1983 the Yashnov (1959) technique modified by Robertson (1970) was used. A calculated correction factor of 1.44 (±3.34) was applied to the 1983 biomass values to permit comparison with the earlier data.

All fish larvae were identified to lowest taxon possible and counted. We herein treat the larvae of six commercially important species (anchoveta [*Engraulis ringens*], Pacific sardine [*Sardinops sagax*], jack mackerel [*Trachurus murphyi*; also known as *T. symmetricus* in U.S.A.], chub mackerel [*Scomber japonicus*], South Pacific menhaden [*Ethmidium maculatum*], and hake [*Merluccius gayi*]) separately from the other 35 identified taxa. These six species are referred to as the "PL" (larvae of pelagic schooling species). The other larval taxa considered together are the "OL". The PL and OL categories are treated separately because abundances of the PL (especially of anchoveta and sardine) mask abundance rela-

FIGURE 1.—Ichthyoplankton study area between Arica and Antofagasta, Chile (18°–24°S), 1964–83.

tions of the OL. The OL are further separated into myctophid, "other mesopelagic" and "coastal" fractions.

Ichthyoplankton abundances are expressed as numbers per 10 m^2 sea surface. Flow meters were not used with the vertical Hensen net hauls; numbers of larvae caught in each tow are multiplied by 30 to provide numbers per 10 m^2 estimates. A flow meter used with WP2 nets provided water volume measurements and more accurate abundance estimates. Based on these measurements the conversion factor applied to Hensen net catches appears to be reasonable: water volumes filtered by 100–0 m vertical WP2 net hauls aver-

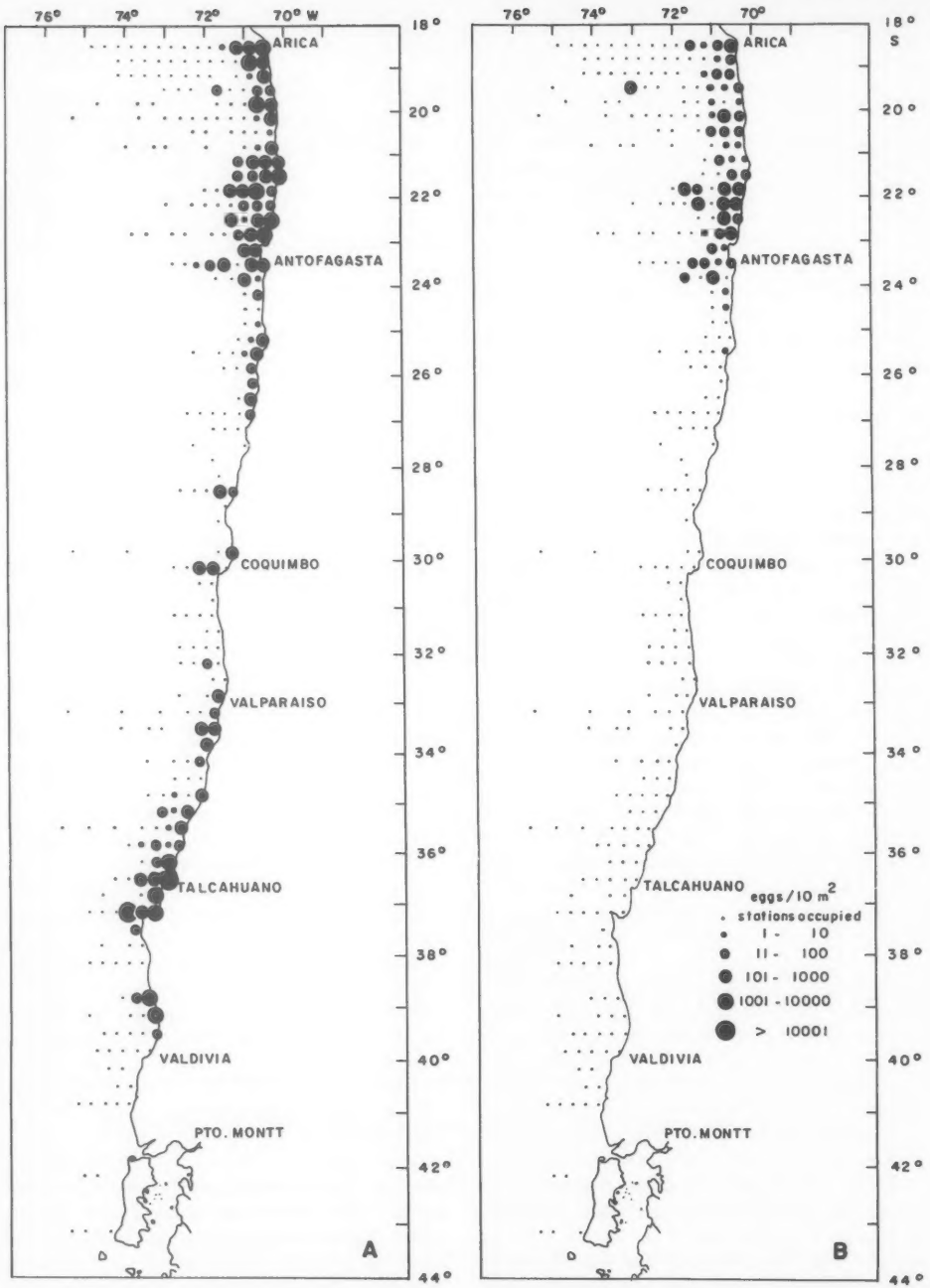

FIGURE 2.—Spawning areas of (A) anchoveta (*Engraulis ringens*) and (B) sardine (*Sardinops sagax*) off Chile based on egg abundances during July–September ichthyoplankton surveys, 1964–73.

TABLE 1.—Cruises yielding samples used for examination of ichthyoplankton abundance and composition variations off northern Chile. Only samples from 18°–24°S are used for interannual comparisons. Data from two 1968 cruises are combined; data from cruise 71(4)69CD are used for analysis of sampling depth-related catch differences. *N* = number of samples used in ichthyoplankton analyses. Tow types: H = Hensen net; WP2 = WP2 net; V = vertical.

Year	Cruise	Dates	Location		*N*	Tow	Type	Depth (m)
1964	06(3)64GE	16/08-23/09	18°20′, 23°38′S	70°11′, 71°50′W	68	H	V	0–50
1965	13(3)65CD	15/08-09/09	18°20′, 23°50′S	70°00′, 72°08′W	76	H	V	0–50
1966	25(3)66CD	21/08-31/09	18°28′, 23°52′S	70°16′, 72°16′W	72	H	V	0–50
1967	37(3)67CD	17/08-10/09	18°25′, 23°45′S	70°05′, 71°38′W	59	H	V	0–50
1968	47(3)68NO	25/08	18°28′, 23°00′S	70°05′, 70°58′W	37	H	V	0–50
	49(3)68NO	29/09	18°26′, 23°01′S	70°11′, 70°59′W	41	H	V	0–50
1969	70(3)69NO	23/08-25/08	18°29′, 23°01′S	70°09′, 71°10′W	35	H	V	0–50
	71(4)69CD	03/12-17/12	28°29′, 38°00′S	71°22′, 73°55′W	43	H	V	0–100
	71(4)69CD	03/12-17/12	28°29′, 38°00′S	71°22′, 73°55′W	39	H	V	0–50
1970	86(3)70NO	25/09-26/09	19°27′, 21°58′S	70°14′, 71°03′W	21	H	V	0–50
1972	109(3)72NO	04/09-15/09	18°29′, 22°58′S	70°10′, 71°25′W	87	H	V	0–50
1973	130(3)73CP	28/07-08/08	18°17′, 23°08′S	70°05′, 72°20′W	42	H	V	0–100
1983	277(3)83CP	07/08-15/09	18°33′, 23°48′S	70°09′, 71°38′W	38	WP2	V	0–100

aged 28.3 m^3 yielding a raw count to numbers per 10 m^2 conversion factor of 35; this 17% increase in conversion factor is associated with a 12% decrease in mouth opening of WP2 vs. Hensen nets. Larval fish diversity is expressed as total numbers of taxa per sampling period and mean numbers of taxa per tow.

Various parametric and nonparametric tests were used for statistical analyses. Differences in mean abundances are tested with 2-tailed *Z* tests and Mann Whitney U tests (Dixon and Massey 1969; Conover 1971). Similarity of abundance ranks within data sets are tested with Kendall's concordance (*W*) test (Tate and Clelland 1969) and Spearman's rho (ρ) correlation test (Conover 1971). Significant values resulting from these tests are indicated, but due to multiple testing these values should be used only as indicators of the relative strengths of relationships. Percent similarity indices (PSI; Whittaker 1975) are used for comparisons of species percentage composition. Because PSIs are strongly influenced by abundant species, we apply these tests to the OL fraction as well as to total larvae. We define as "high" all PSI values ≥80, as "moderate" PSI's ≥65 and <80, and as "low" values <65.

SAMPLING CONSIDERATIONS

Sampling Depth Differences

The 100 m sampling depths in 1973 and 1983 potentially effect direct comparisons of abundance estimates and species composition in these vs. earlier data sets owing to individual species' depth distributions. Evaluation of depth-related sampling differences is possible through a comparison of data obtained from coincidental 50–0 m and 100–0 m Hensen net samples taken during December 1969 at 28°–38°S (Table 1). These data indicate that abundance estimates and percentage contribution of the PL to total larvae were higher in 50 m tows while those of the OL were higher in 100 m tows (Table 2). Four of five PL species caught were more abundant and frequent in the 50 m samples. The greatest differences were for *Trachurus murphyi*, which was 5× more abundant and 3.6× more frequent, and *Merluccius gayi*, which was present only in 50 m samples. Abundance estimates were higher for 11 of 16 OL taxa in 100 m tows although, with a few exceptions, catch frequencies were similar. The greatest difference was for *Triphoturus mexi-*

TABLE 2.—Catch comparisons of 50–0 m and 100–0 m Hensen net tows taken at lat. 28°–38°S, long. 71°–74°W during 3–17 December 1969. Abundances expressed as mean and standard deviations of numbers per 10 m^2. F = percent frequency of occurrence in samples. Depth-related catch differences are shown as ratios of 50:100 m abundance estimates, species percentage contribution to total identified larvae, PL and OL percentage contribution to total larvae, and taxonomic diversity (mean numbers per tow and total numbers of taxa). *N* = number of samples. PL = larvae of pelagic species; OL = other larval taxa.

	50–0 m (*N* = 43)				100–0 m (*N* = 39)				
Taxon	$\bar{X}$	(S)	F	%	$\bar{X}$	(S)	F	%	Ratio
Engraulis ringens	34.2	(122.8)	23.2	13.42	22.3	(69.4)	15.4	7.23	1.53
Clupea bentincki	6.3	(28.2)	9.3	2.47	1.5	(6.7)	5.1	0.49	4.20
Ethmidium maculatum	0.7	(4.6)	2.3	0.27	0.8	(4.8)	2.6	0.26	0.88
Merluccius gayi	1.4	(6.4)	4.6	0.55					
Trachurus murphyi	4.2	(14.0)	9.3	1.65	0.8	(4.8)	2.6	0.26	5.25
Total PL	46.8	(131.1)	34.9	18.36	25.4	(71.0)	23.1	8.24	1.84
Bathylagus nigrigenys	0.7	(4.6)	2.3	0.27	0.8	(4.8)	2.6	0.26	0.88
Vinciguerria lucetia	10.5	(33.9)	14.0	4.12	16.9	(75.6)	7.7	5.48	0.62
Diogenichthys spp.	31.4	(107.0)	20.9	12.32	37.7	(79.9)	28.2	12.22	0.83
Hygophum bruuni	121.4	(238.2)	58.1	47.64	166.2	(291.0)	53.8	53.86	0.73
Protomyctophum sp.					3.1	(9.2)	10.3	1.00	
Diaphus sp.	7.7	(18.6)	18.6	3.02	9.2	(24.0)	17.9	2.98	0.84
Lampanyctus parvicauda	7.7	(18.6)	16.3	3.02	6.9	(21.2)	15.4	2.24	1.12
Lampanyctus sp.	1.4	(6.4)	4.6	0.55	1.5	(6.7)	5.1	0.49	0.93
Triphoturus mexicanus	7.7	(21.8)	14.0	3.02	18.5	(57.4)	20.5	5.99	0.42
Scopelosaurus sp.					0.8	(4.8)	2.6	0.26	
Normanichthys crockeri	15.3	(38.9)	18.6	6.00	20.0	(66.5)	10.3	6.48	0.76
Sebastes sp.	1.4	(9.1)	2.3	0.55	0.8	(4.8)	2.6	0.26	1.75
Blenniid A	0.7	(4.6)	2.3	0.27					
Blenniid D	0.7	(4.6)	2.3	0.27	0.8	(4.8)	2.6	0.26	0.88
Bothid	0.7	(4.6)	2.3	0.27					
Unid. 2	0.7	(4.6)	2.3	0.27					
Small damaged myctophids	4.8				9.2				
Other unidentified	13.2				7.0				
Total OL	226.0	(316.0)	86.0	81.59	299.4	(405.9)	82.0	91.78	0.84
Total larvae	272.8	(340.7)			324.8	(400.0)			0.84
No. taxa/tow	2.5	(2.0)			2.2	(2.0)			1.13
Total no. taxa	18				17				0.94

canus which was 2.4× more abundant and 1.5× more frequent in 100 m tows. Because of the large catch variability, none of the species abundance differences nor the abundance differences of the PL, OL, and total larvae are significant (*Z* tests, *P*'s all >0.10). Additionally, species abundances within all positive tows from the two sampling depths are not significantly different (Mann Whitney U tests, $P > 0.10$ in all cases).

The overall species composition of 50 and 100 m tows was similar. Despite greater proportions of PL in 50 m tows, the PSI value from comparisons of total species lists was high (87.7). Species percentage contribution within the OL fraction of the two tow types was also quite similar (94.5). Species abundance rankings within the two total larval data sets are significantly correlated ($\rho = +0.80$; $P < 0.01$). Species diversity estimates (total numbers of taxa and mean numbers of taxa per tow) are also similar.

From these comparisons it is apparent that the PL predominantly occur within the upper 50 m. Similar shallow (e.g., ≤50 m) distributions have been described for dominant PL species off of Peru (anchoveta, sardine, and hake; Sameoto 1982). The generally lower 100 m abundance estimates of these species is puzzling, but suggests possibly shorter sampling time and/or less efficient sampling within the upper 50 m of these tows. Higher catch frequency and abundance of *T. mexicanus* in 100 m tows suggest that large proportions (e.g., 30–60%) of these larvae are at 50–100 m.

As a result of these catch differences we suggest caution in making direct numerical comparisons between the 1973 and 1983 vs. earlier data sets. Although the overall compositions and abundance relations should not be markedly altered, some accommodation should be allowed for the percentage contributions and across-year abundance ranks of PL species (especially *Trachurus*) and *Triphoturus mexicanus*.

Net Type Differences

There are no data available for a direct evaluation of catch differences between the vertical Hensen and WP2 net tows. However, comparisons of data from the 1983 WP2 net hauls (Table 3) do not indicate that this net is more or less efficient than the Hensen net. Mean abundances and species diversity (total numbers of taxa and mean numbers of taxa per tow) are within the ranges of values from Hensen net tows.

Day-Night Catch Considerations

Day and night sample data have been combined for each cruise. Day samples (0600–1800 hours) outnumbered (generally 55–64%) night samples during all cruises. In nine cases there were non-significant day-night larval catch differences (Z tests, $P > 0.05$) and overall similarity in night: day catch ratios (0.74–1.8:1; mode = 1.2:1). One cruise had a significantly higher night vs. day catch (2.5×; $P < 0.01$); this cruise and one with

TABLE 3.—Abundance estimates and diversity of larval fishes and abundance estimates of zooplankton collected in July-September samples off northern Chile (18°–24°S), 1964–83. Larval fish abundances as mean numbers per 10 m². PL = larvae of commercially important pelagic species; OL = other larval taxa (myctophid, other mesopelagic, and other categories). Number of larvae is total raw count of identified larvae for each sampling period. Larval fish diversity expressed as total number of identified taxa and mean number of taxa per tow. Zooplankton abundance is mean displacement volume (cc/10 m²). N.A. = data not available.

	Mean abundance for									
Taxon	1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
Engraulis ringens	302.0	36.7	3,478.3	224.7	72.3	181.7	620.0	1,634.1	1,816.4	—
Sardinops sagax	5.3	5.1	12.5	4.6	21.1	24.9	1.4	327.2	52.1	594.9
Ethmidium maculatum	—	—	—	—	—	2.6	—	0.7	—	—
Trachurus murphyi	2.6	7.1	10.8	3.1	0.4	6.8	5.7	100.3	2.1	—
Scomber japonicus	—	0.4	—	—	—	—	—	25.9	—	—
Merluccius gayi	—	—	—	—	—	—	—	—	0.7	2.6
Total PL	309.9	49.3	3,501.6	232.4	93.8	216.0	627.1	2,088.2	1,871.3	597.5
Bathylagus nigrigenys	4.0	5.1	6.7	9.7	6.2	0.9	7.2	56.6	35.0	31.5
Vinciguerria lucetia	3.1	0.4	2.9	6.1	3.1	2.6	21.4	54.8	18.6	3.7
Sternoptyx diaphana	—	—	—	—	—	—	—	0.7	0.7	1.0
Chauliodus sp.	—	—	—	—	—	—	—	0.3	—	—
Stomias spp.	—	—	—	—	—	—	—	—	—	1.9
Lestidiops pacificum	—	—	—	—	—	—	—	0.3	0.7	—
Melamphaes sp.	—	—	—	0.5	0.4	—	—	0.3	2.1	—
Beryciform	—	—	—	—	—	—	1.4	—	—	—
Other mesopelagics	7.1	5.5	9.6	16.3	9.7	3.5	30.0	113.0	57.1	38.1
Diogenichthys spp.	6.2	18.9	14.6	30.5	7.3	14.6	21.4	59.3	39.3	114.2
Hygophum bruuni	—	2.8	1.2	3.6	—	—	—	—	—	0.9
Hygophum atratum	—	—	—	—	—	—	—	—	—	6.7
Metelectrona ventralis	—	—	—	—	—	—	—	—	—	0.9
Myctophum nitidulum	0.4	—	0.4	—	0.4	0.9	—	4.8	4.3	4.6
Diaphus sp.	—	0.4	0.4	—	—	—	1.4	0.3	—	4.5
Lampanyctus parvicauda	41.0	32.0	65.8	63.0	10.8	38.6	5.7	29.7	12.1	15.5
Lampanyctus spp.	—	—	0.8	—	1.1	—	—	—	0.7	—
Triphoturus mexicanus	31.8	15.8	20.8	29.0	4.6	31.7	11.4	19.7	23.6	33.6
Myctophids	79.4	69.9	104.0	126.1	24.2	85.8	39.9	113.8	80.0	100.9
Normanichtys crockeri	17.2	1.5	281.2	5.6	2.3	26.6	10.0	2.4	31.4	—
Sebastes sp.	0.4	—	2.5	1.0	0.8	—	—	—	0.7	—
Gadiform D	—	—	0.8	—	—	—	—	—	—	—
Macrourid A	—	—	—	0.5	—	—	—	—	0.7	—
Macrourid C	—	—	—	0.5	—	—	—	—	—	—
Blenniid A	0.4	—	0.8	—	1.2	—	—	—	1.4	—
Blenniid B	—	—	0.4	—	—	—	—	—	—	—
Blenniid C	—	—	—	1.5	—	—	—	0.3	—	—
Blenniid D	5.3	0.4	16.7	7.1	4.2	2.6	—	2.8	8.6	1.0
Gobiesocid A	0.4	—	0.8	—	—	—	—	1.0	0.7	—
Gobiesocid B	—	—	—	—	0.4	—	—	—	—	—
Unid. 1	—	—	—	—	0.8	—	—	—	5.7	8.6
Unid. 2	—	—	0.4	—	—	—	—	0.3	12.1	—
Unid. 3	—	—	—	—	0.4	1.7	—	0.3	0.7	—
Unid. 4	—	—	—	—	—	—	—	0.3	0.7	—
Ophidiid	—	—	—	1.0	0.8	—	—	—	—	—
Hippoglossina sp.	—	—	—	—	—	—	—	0.3	—	—
Other larvae	23.7	1.9	303.6	17.2	10.9	30.9	10.0	7.7	62.7	9.6
Total OL	110.2	77.3	417.2	159.6	44.8	120.2	79.9	234.5	199.8	228.4

TABLE 3.—*Continued.*

Taxon	Mean abundance for 1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
Larval fish abundance and diversity										
Total ID PL	309.9	49.3	3,501.6	232.4	93.8	216.0	627.1	2,088.2	1,871.3	597.5
Total ID OL	110.2	77.3	417.2	159.6	44.8	120.2	79.9	234.5	199.8	228.6
Total ID larvae	420.1	126.6	3,918.8	392.0	138.6	336.2	707.0	2,322.7	2,071.1	826.1
Unid/missing OL	10.2	4.4	17.0	22.0	3.4	11.9	7.2	104.5	57.2	76.6
Total larvae	430.3	131.0	3,935.8	414.0	142.0	348.1	714.2	2,427.2	2,128.3	902.7
Number of larvae	953	321	9,406	771	360	650	495	6,738	2,900	893
Number of taxa	15	14	20	19	20	13	12	26	25	19
Number of taxa/tow	2.2	1.6	3.2	2.5	1.4	1.9	2.3	5.3	4.1	3.7
Number of samples	68	76	72	59	78	35	21	87	42	38
Zooplankton abundance	333.9	242.2	406.5	370.8	279.2	141.0	N.A.	301.7	100.6	168.7
Number of samples	85	124	72	59	78	35		110	42	30

a 1.8:1 night:day catch ratio were represented by fairly equal day (55–57%) and night samples.

TAXONOMIC PROBLEMS

The 576 samples used for interannual comparisons yielded a total of 41 taxa including 19 species, 7 genera, and 11 higher taxa (Table 4). The PL and most mesopelagic forms were identified to species. During several cruises there were large proportions of small *Diogenichthys* spp. (Myctophidae) larvae which could not be identified to species. As a consequence, data on the two species, *D. atlanticus* and *D. laternatus*, were lumped to permit reasonable between-year taxonomic composition comparisons. In all but one cruise, *D. laternatus* dominated (77–100%) the identifiable *Diogenichthys* larvae. Total within-year *Diogenichthys* spp. abundances were multiplied by proportions of identified *D. laternatus* and *D. atlanticus* larvae to provide between-year abundance rankings for each species.

Species identifications of coastal forms are limited by inadequate taxonomic information and by the presence of generally early larval developmental stages in samples. These larvae are primarily classified at familial and ordinal levels. Because the classifications include few multispecies groupings and those were numerically rare the taxonomic limitations offer no severe analytical problems.

Largest taxonomic problems occurred in cruises when large numbers of small unidentifiable larvae were caught (e.g., 1972 and 1983; Table 3). Additionally, most cruises had "missing" larvae (e.g., "other larvae" enumerated when the samples were first processed but not accounted for during later species identification work). With the exception of 1983 the unidentified and missing larvae made up ≤5% of the total larval abundance for each sampling period.

RESULTS

Overall Ichthyoplankton Composition

The 576 July–September samples used for interannual comparisons yielded a total of 23,487 identified larvae. These larvae were dominated (85.1%) by PL species (Table 4). Overall dominants were anchoveta (*Engraulis ringens;* 74.3%) and sardine (*Sardinops sagax*; 9.3%). The other PL species were relatively rare: *Trachurus murphyi* contributed 1.2% and *Scomber japonicus, Merluccius gayi*, and *Ethmidium maculatum* together formed 0.3% of the total. The larval abundances of these species off of Chile are strongly influenced by sampling time and location. *Merluccius gayi* occurs primarily to the south of the study area (24°–43°S) and *Scomber japonicus* and *Trachurus murphyi* have later summer (November–February) spawning peaks.

The OL were dominated by mesopelagic fishes (18 taxa, 10.6% of total larvae). Myctophids were most abundant (8.0%) primarily because of the large numbers of *Diogenichthys* spp., *Lampanyctus parvicauda*, and *Triphoturus mexicanus*, which together made up 7.7% of the total. One bathylagid (*Bathylagus nigrigenys*) and one gonostomatid (*Vinciguerria lucetia*) were also relatively abundant (together 2.5%). Coastal fish larvae (14 taxa) made up 4.2% of the total; a scorpaeniform (*Normanichthys crockeri*; 3.4%) and blenniid (Blenniid D; 0.4%) dominated this group.

Eighteen taxa were relatively frequent (e.g., in

≥50% of cruises) and/or abundant across the 10 sampling periods (Table 4). These taxa (four PL species, seven myctophid taxa, two other mesopelagic species, and five coastal forms) made up 99.6% of the identified larvae; they also contributed 97–100% of the identified larvae (91.2–99.6% of total larvae) and included the top 9–12 ranked taxa within each sampling period (Table 5).

TABLE 4.—Ichthyoplankton species collected in July-September samples off northern Chile (18°–24°S, 70°–72°W), 1964–83. Relative abundance (ROA) and percentage composition based on summed cruise mean abundances (no./10 m²) of all identified forms. Frequency is number of total 10 sampling periods when taxon was caught. Categories are PL (commercially important pelagic species) and other taxonomic components (M = myctophids; OM = other mesopelagic taxa; C = coastal forms).

Taxon	ROA	%	Frequency	Category
Engraulis ringens	1	74.29	9	PL
Sardinops sagax	2	9.33	10	PL
Normanichthys crockeri	3	3.36	9	C
Diogenichthys laternatus + *D. atlanticus*	4	2.90	10	M
Lampanyctus parvicauda	5	2.79	10	M
Triphoturus mexicanus	6	1.97	10	M
Bathylagus nigrigenys	7	1.44	10	OM
Trachurus murphyi	8	1.23	9	PL
Vinciguerria lucetia	9	1.04	10	OM
Blenniid D	10	0.43	9	C
Scomber japonicus	11	0.23	2	PL
Myctophum nitidulum	12	0.14	7	M
Unid. 1	13	0.13	3	C
Unid. 2	14	0.11	3	C
Hygophum bruuni	15	0.075	4	M
Diaphus sp.	16	0.062	5	M
Hygophum atratum	17	0.060	1	M
Sebastes sp.	18	0.050	5	C
Blenniid A	19	0.034	4	C
Ethmidium maculatum	20.5	0.030	1	PL
Merluccius gayi	20.5	0.030	2	PL
Unid. 3	22	0.028	4	C
Melamphaes sp.	23.5	0.026	3	OM
Gobiesocid A	23.5	0.026	4	C
Lampanyctus spp.	25	0.024	3	M
Sternoptyx diaphana	26	0.020	3	OM
Stomias spp.	27	0.017	1	OM
Blenniid C	28.5	0.016	2	C
Ophidiid	28.5	0.016	2	C
Beryciform	30	0.012	1	OM
Macrourid A	31	0.011	2	
Lestidiops pacificum	32.5	0.009	2	OM
Unid. 4	32.5	0.009	2	C
Metelectrona ventralis	34	0.008	1	M
Gadiform D	35	0.007	1	
Macrourid C	36	0.004	1	
Blenniid B	37.5	0.0036	1	C
Gobiesocid B	37.5	0.0036	1	C
Chauliodus sp.	39.5	0.0030	1	OM
Hippoglossina sp.	39.5	0.0030	1	C
Total number of identified larvae:		23,487		
Total number of samples:		576		
Total number of taxa:		41		

INTERANNUAL VARIATIONS IN ABUNDANCE AND COMPOSITION

The ichthyoplankton demonstrated extreme interannual variations in abundance and composition (Tables 3, 5; Fig. 3A, B). Most obvious are the 1) total larval and PL abundance peaks of 1966, 1972, and 1973 and 2) shift from anchoveta to sardine dominance between 1973 and 1983. The maximum total larval abundance values in 1966, 1972, and 1973 were 2.4–30× higher than those of other years; the PL had 3–71× higher abundances during these vs. other years. Interannual abundance variations during the seven years of lower abundance were also large for total larvae (to 6.9×) and the PL (to 12.7×). Anchoveta dominated the ichthyoplankton through 1973 (29.0–88.8%) and was directly responsible for the extreme abundance variations; anchoveta were absent from the 1983 samples, and sardine larvae (72.0%) contributed to the moderately high total larval and PL abundances (Table 5).

The OL fraction had less extreme abundance variations than the PL: maximum 1966, 1972, 1973, and 1983 mean abundance values ranged from 1.4 to 9× those of the other years; mean values within the six years of lower abundance varied to 3.8×. Unlike the PL, OL abundance fluctuations were not attributed to any one taxonomic component (Fig. 3B): the 1966 peak was largely due to coastal taxa (73% of OL); myctophids and other mesopelagic taxa equally dominated the 1972 peak (48%); myctophids dominated (79%) in 1983; and all three components were relatively abundant (29–40%) in 1973. Myctophids were generally the dominant component (50–90%) during the six years of lower OL abundance. Abundance fluctuations (as range of mean abundance values) across the 10 years were less extreme for myctophids (8.1×) than for the other mesopelagic taxa (32.3×) and coastal forms (160×).

In contrast to the ichthyoplankton, July–September zooplankton biomass values were relatively constant between years and exhibited only a 4× range in values (Table 3).

Despite large between-year variability in relative proportions of the PL and OL, there is a significant agreement of their ranked mean abundances across the 10 years ($\rho = +0.81$, $P < 0.01$). There is also a general agreement of the ranked mean abundances of PL and the three OL components across the 10 years ($W = 0.44$; $P = 0.05$). These categories were generally more abundant

TABLE 5.—Comparisons of relative abundances of dominant larval fish taxa collected off of northern Chile (18°–24°S, 70°–72°W) during July-September sampling periods, 1964–83. Relative abundances within each year are presented as (A) percentage contribution to total identified larvae and (B) ranked abundance. Taxa are listed in order of total summed 10-yr mean abundances.

Taxon	1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
A. Percentage contribution to total identified larvae										
Engraulis ringens	71.89	28.99	88.76	57.32	52.20	54.05	87.69	70.35	87.70	—
Sardinops sagax	1.26	4.03	0.32	1.17	15.23	7.41	0.20	14.09	2.52	72.01
Normanichthys crockeri	4.09	1.18	7.18	1.43	1.66	7.91	1.41	0.10	1.52	—
Diogenichthys spp.	1.48	14.93	0.37	7.78	5.27	4.34	3.03	2.55	1.90	13.82
Lampanyctus parvicauda	9.76	25.28	1.68	16.07	7.80	11.48	0.81	1.28	0.58	1.88
Triphoturus mexicanus	7.57	12.48	0.53	7.40	3.32	9.43	1.61	0.85	1.14	4.07
Bathylagus nigrigenys	0.95	4.03	0.17	2.47	4.48	0.27	1.02	2.44	1.69	3.81
Trachurus murphyi	0.62	5.61	0.28	0.79	0.29	2.02	0.81	4.32	0.10	—
Vinciguerria lucetia	0.74	0.32	0.07	1.56	2.24	0.77	3.03	2.36	0.90	0.45
Blenniid D	1.26	0.32	0.43	1.81	3.03	0.77	—	0.12	0.42	0.12
Scomber japonicus	—	0.32	—	—	—	—	—	1.12	—	—
Myctophum nitidulum	0.10	—	0.01	—	0.29	0.27	—	0.21	0.21	0.56
Unid. 1	—	—	—	—	0.56	—	—	—	0.27	0.96
Unid. 2	—	—	0.01	—	—	—	—	0.01	0.57	—
Hygophum bruuni	—	2.21	0.03	0.92	—	—	—	—	—	0.11
Diaphus sp.	—	0.32	0.01	—	—	—	0.20	0.01	—	0.54
Hygophum atratum	—	—	—	—	—	—	—	—	—	0.81
Sebastes sp.	0.10	—	0.06	0.26	0.58	—	—	—	0.03	—
Other taxa	0.19	—	0.09	1.02	3.03	1.28	0.20	0.19	0.43	0.78
B. Ranked within-year abundance										
Engraulis ringens	1	1	1	1	1	1	1	1	1	—
Sardinops sagax	6.5	6.5	7	9	2	5	10	2	2	1
Normanichthys crockeri	4	9	2	8	9	4	5	12	5	—
Diogenichthys spp.	5	3	6	3	4	6	2.5	4	3	2
Lampanyctus parvicauda	2	2	3	2	3	2	7.5	7	8.5	5
Triphoturus mexicanus	3	4	4	4	6	3	4	9	6	3
Bathylagus nigrigenys	8	6.5	9	5	5	12.5	6	5	4	4
Trachurus murphyi	10	5	8	11	17	7	7.5	3	13.5	—
Vinciguerria lucetia	9	11.5	10	7	8	9	2.5	6	7	10
Blenniid D	6.5	11.5	5	6	7	9	—	11	10	13.5
Scomber japonicus	—	11.5	—	—	—	—	—	8	—	—
Myctophum nitidulum	12.5	—	18.5	—	17	12.5	—	10	12	8
Unid. 1	—	—	—	—	12.5	—	—	—	11	6
Unid. 2	—	—	18.5	—	—	—	—	20.5	8.5	—
Hygophum bruuni	—	8	12	10	—	—	—	—	—	15.5
Diaphus sp.	—	11.5	18.5	—	—	—	10	20.5	—	9
Hygophum atratum	—	—	—	—	—	—	—	—	—	7
Sebastes sp.	12.5	—	11	13.5	14	—	—	—	21	—

in 1966, 1972, and 1973 and relatively rare in 1965 and 1968. The ranked abundance patterns of each of the components differ from one another (e.g., all pairwise correlation coefficients [$\rho = -0.21$ to $+0.61$] are nonsignificant). Larval diversity is strongly correlated with total larval abundance ($\rho = +0.88$, $P < 0.01$).

There are no significant correlations between abundance ranks of invertebrate zooplankton biomass and total larvae ($\rho = +0.27$) or any of the larval categories ($\rho = -0.03$ to $+0.22$; $P > 0.05$ in all cases).

Species Abundance Variations and Relations

The top 10 ranking larval fish taxa were caught during at least 9 of the 10 sampling periods (Table 4). All of these taxa exhibited large interannual abundance fluctuations (Table 3). Most marked were the abundance changes of anchoveta, sardine, and coastal species *Normanichthys crockeri*. This latter species (rank 3 in overall abundance) was frequently abundant prior to 1983; like anchoveta it was absent from 1983 samples. Among the 10 taxa only *Triphoturus mexicanus* had <10× changes in mean abundance values; <20× changes occurred for *Lampanyctus parvicauda* (11.5×) and *Diogenichthys* spp. (18.4×); all other taxa had >20× mean abundance changes over the 10 years. The abundance fluctuations of these 10 taxa are primarily responsible for the interannual abundance and composition variations (Table 5; Fig. 3A, B).

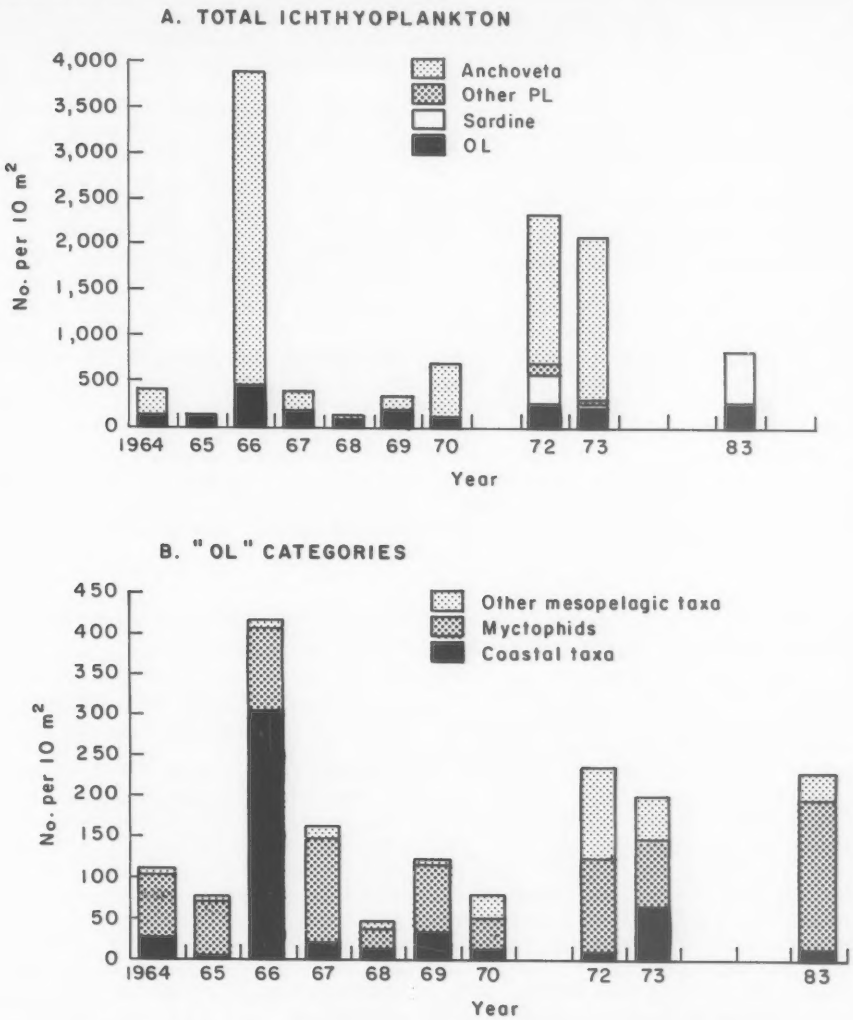

FIGURE 3.—Mean abundance (numbers per 10 m^2) of (A) total ichthyoplankton and major PL components and (B) total OL and major OL components collected off northern Chile (18°–24°S) during July–September sampling periods, 1964–83.

Between-year comparisons of the species percentage compositions of total larvae give a wide range of PSI values (3.3–95.0; Table 6A) which primarily reflect similarity in percentages of anchoveta; 51% of these values are moderate to high (e.g., ≥65). Highest values (91.5–95.0) come from comparisons between 1966, 1970, and 1973 when anchoveta contributed >87% of the larvae. High values (80.7–82.5) also result from comparisons between 1964, 1967, and 1969 and result from moderate anchoveta abundance (54.0–71.9%) and relatively similar proportions of other taxa. Lowest values (3.3–31.0) result from comparisons of 1983 vs. all other years and reflect the absence of anchoveta larvae in 1983 samples. The 1973 and 1983 PSI values are little affected (e.g., ≤2.3) by

TABLE 6.—Between-year percent similarity index (PSI) values from comparisons of (A) total larvae and (B) the OL (other larval taxa) fraction collected during July–September sampling periods off northern Chile (18°–24°S), 1964–83.

	PSI values for								
	1965	1966	1967	1968	1969	1970	1972	1973	1983
A. Total larvae									
1964	52.44	79.94	82.22	71.25	80.70	79.70	77.89	80.30	10.30
1965	X	33.95	67.41	55.54	62.38	38.16	45.32	38.74	28.47
1966		X	62.69	57.83	65.08	91.55	73.65	91.88	3.32
1967			X	77.96	82.47	67.75	68.21	66.82	18.05
1968				X	79.39	62.81	76.39	63.68	30.95
1969					X	62.95	69.67	63.50	18.80
1970						X	79.06	94.95	7.31
1972							X	79.42	22.02
1973								X	8.95
B. OL fraction									
1964	69.88	47.01	75.76	57.56	85.16	45.99	36.08	51.29	33.15
1965	X	29.22	88.07	60.36	68.42	55.43	54.30	47.13	54.39
1966		X	34.96	36.78	50.09	30.53	26.15	37.50	18.48
1967			X	70.21	71.01	53.92	52.55	55.68	49.12
1968				X	58.46	54.85	61.57	67.92	51.92
1969					X	48.98	39.22	51.92	37.18
1970						X	74.35	68.40	60.21
1972							X	66.23	58.74
1973								X	58.61

accommodations for possible sampling depth-catch differences of *Trachurus gayi* and *Triphoturus mexicanus*.

When the PL are excluded, comparisons between the OL taxa yield generally lower PSI values than those of the total larvae; only 24% of the 18.5–88.1 values are moderate to high (Table 6B). Moderate to high values (69.9–88.1) come from comparisons between 1964, 1965, 1967, and 1969, and in part result from similar proportions of *Lampanyctus parvicauda* (32.1–41.4%) and *Triphoturus mexicanus* (18.2–28.9%) during those years. Moderate values (66.2–74.4) also come from comparisons of 1967 vs. 1968 and 1969 (similar proportions of *L. parvicauda, T. mexicanus*, and *Diogenichthys* [12.2–39.5%]); 1970 vs. 1972 (similar proportions of *Vinciguerria lucetia* and *Diogenichthys* [23.4–26.8%]); and 1972 vs. 1973 (similar proportions of *Bathylagus nigrigenys, V. lucetia*, and *Diogenichthys* [9.3–25.3%]). Lowest PSI values (<30) result from comparisons of 1966 vs. 1965, 1970, 1972, and 1983, and are due largely to extreme dominance by *Normanichthys crockeri* (67.4% of OL) in 1966. Recalculations to accommodate for possible depth-related increased catches of *T. mexicanus* in most cases decrease 1973 and 1983 PSI values (e.g., by 2.6–7.2) and in two cases (1968 and 1970 vs. 1973) change the value characterization from moderate (67.9 and 68.4) to low (63.8 and 64.5). With one exception (1972 vs. 1973, PSI = 67.0) all of the other adjusted values are low.

Species Across-Year Ranked Abundance Patterns

Individual species across-year abundance rankings demonstrate a variety of patterns. Three patterns are shared by nine of the more frequently occurring taxa (Table 7). These involve 1) a group formed by anchoveta and three coastal forms; 2) a group formed by one myctophid and two other mesopelagic species; and 3) a species pair consisting of sardine and a myctophid. Another species pair (two myctophids) can be formed if the 1973 and 1983 abundances of *T. mexicanus* are adjusted.

Group I includes anchoveta, *Normanichthys crockeri*, Blenniid D, and *Sebastes* sp. (Table 7). There is a significant concordance among these species as to years of highest (1966 and 1973) and lowest (1965 and 1983) abundance ($W = 0.69$, $P < 0.01$). The abundance rankings of anchoveta and *N. crockeri* ($\rho = +0.79$) and of Blenniid D and *Sebastes* ($\rho = +0.88$) are significantly correlated ($P \leq 0.01$). None of the correlations between species of the two pairs are significant due to differences in 1967–68 vs. 1970–72 relative abundances.

The three Group II species, *Diogenichthys later-*

natus, Bathylagus nigrigenys, and *Vinciguerria lucetia*, have a concordance of higher abundances in 1972, 1973, and 1983 vs. other years ($W = 0.81$, $P < 0.01$). The abundance rankings of *B. nigrigenys* are strongly correlated with those of *D. laternatus* and *V. lucetia* ($\rho = +0.82$, $P < 0.01$ in both cases); the correlation between *D. laternatus* and *V. lucetia* is not significant.

The abundance rankings of sardine and *Myctophum nitidulum* (Pair I species) are significantly correlated ($\rho = +0.96$, $P < 0.01$); both species were rare or absent in 1970 and most abundant in 1972, 1973, and 1983.

With adjustment to 1973 and 1983 abundances of *T. mexicanus*, its abundance rankings are strongly correlated with those of *Lampanyctus parvicauda* (Pair II species; $\rho = +0.84$, $P < 0.01$). Highest relative abundances of both species were in 1964, 1966, 1967, and 1969.

Three relatively frequent species (*Trachurus murphyi, Diogenichthys atlanticus*, and *Diaphus* sp.) do not conform to any of the above patterns. If the 1973 *Trachurus* abundance is adjusted to accommodate for possible undersampling, its abundance pattern is similar to that of anchoveta ($\rho = +0.68$, $P = 0.05$) but not to any of the other Group I species ($\rho = +0.03$ to $+0.46$).

VARIATIONS IN ABUNDANCE AND COMPOSITION RELATIVE TO HYDROGRAPHIC CONDITIONS

Ichthyoplankton abundances in the 10 years sampled show no consistent patterns relative to warm water-cold water events (Table 8). High PL and OL abundances occurred during strong El Niño events (1972 and 1983) and during cold or transition years immediately following El Niños (1966 and 1973). Lowest abundances of both fractions were associated with the 1965 El Niño and warm 1968. Neither the PL nor OL have significant correlations with ranked (high to low) July–

TABLE 7.—Larval fish taxa grouped according to similar across-year (1964–83) ranked abundance patterns. Significant agreement of group rankings indicated by Kendall's concordance (W) values. Correlations between species pair rankings indicated by Spearman's rho (ρ) values. Significant values at $P \leq 0.05$ are indicated, but note use of multiple testing. ** = abundance ranks adjusted to accommodate for possible sampling depth related catch differences (Table 2).

	Abundance rank for									
Species	1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
Group I										
Engraulis ringens	5	9	1	6	8	7	4	3	2	10
Normanichthys crockeri	4	9	1	6	8	3	5	7	2	10
Blenniid D	4	9	1	3	5	7	10	6	2	8
Sebastes sp.	5	8	1	2	3	8	8	8	4	8
		$W = 0.69$ ($P < 0.01$)								
E. ringens-N. crockeri		$\rho = +0.79$ ($P = 0.01$)								
Blenniid D-*Sebastes* sp.		$\rho = +0.88$ ($P < 0.01$)								
E. ringens-Blenniid D		$\rho = +0.59$								
E. ringens-Sebastes sp.		$\rho = +0.44$								
N. crockeri-Blenniid D		$\rho = +0.61$								
N. crockeri-Sebastes sp.		$\rho = +0.48$								
Group II										
Diogenichthys laternatus	10	5	7.5	4	9	7.5	6	2	3	1
Bathylagus nigrigenys	9	8	6	4	7	10	5	1	2	3
Vinciguerria lucetia	6.5	10	8	4	6.5	9	2	1	3	5
		$W = 0.81$ ($P < 0.01$)								
B. nigrigenys-D. laternatus		$\rho = +0.82$ ($P < 0.01$)								
B. nigrigenys-V. lucetia		$\rho = +0.82$ ($P < 0.01$)								
D. laternatus-V. lucetia		$\rho = +0.52$								
Pair I										
Sardinops sagax	7	8	6	9	5	4	10	2	3	1
Myctophum nitidulum	6	9	6	9	6	4	9	1	3	2
S. sagax-M. nitidulum		$\rho = +0.96$ ($P < 0.01$)								
Pair II										
Lanpanyctus parvicauda	3	5	1	2	9	4	10	6	8	7
*Triphoturus mexicanus***	1	6	4	3	10	2	8	5	9	7
*L. parvicauda-T. mexicanus***		$\rho = +0.84$ ($P < 0.01$)								

TABLE 8.—Range, mean, standard deviation and ranked (high to low) values of sea ichthyoplankton sampling periods, 1964–83. N = number of observations. N.A. = data not (1976), Bernal et al. (1982), and Kelly and Blanco (1983).

	1964	1965	1966	1967	1968
Temperature (°C)					
N	85	128	72	55	81
Range	13.5–17.9	13.6–18.1	13.7–17.1	13.3–16.0	14.3–18.6
$\bar{X}$	15.7	16.5	15.3	14.8	16.5
(S)	(1.0)	(1.0)	(0.8)	(0.8)	(0.9)
Rank	7	3.5	8	9	3.5
Salinity (‰)					
N	84	124	72	4	81
Range	34.51–34.99	34.80–35.40	34.53–35.03	34.74–34.82	34.69–35.23
$\bar{X}$	34.74	35.06	34.83	34.78	34.92
(S)	(0.12)	(0.12)	(0.11)	(0.04)	(0.12)
Rank	9	2	6	8	4
Hydrographic condition:	Cold	El Niño	Transition	Cold	Warm

September mean temperature and salinity values; larval diversity (mean number of taxa/tow) also shows no correlation with these values (Table 9). Within the PL, anchoveta were most abundant during years immediately following El Niños (cold 1966, transition 1973), the 1972 El Niño, and cold 1970; lowest abundances were during the 1965 and 1983 El Niños (Table 8). There are no significant correlations between ranked anchoveta abundances and ranked values of temperature or salinity (Table 10). Sardine larvae were most abundant during and after the 1972 El Niño; prior to this moderate abundances and relatively large percentage contributions to the ichthyoplankton occurred only during the warm 1968–69 period (Tables 5, 7). Lowest sardine abundances were during cold years 1964, 1967, and 1970 and the 1965 El Niño. Despite low abundances during the 1965 El Niño, there is a significant positive correlation between ranked sardine abundance and temperature ($\rho = +0.69$, $P < 0.05$). Ranked larval anchoveta and sardine abundances are not correlated ($\rho = -0.07$).

The only apparent warm-cold year abundance pattern among the OL categories is that of the coastal taxa; this group had lowest abundances during the 1965, 1972, and 1983 El Niños and highest abundances in subsequent 1966 and 1973 transition years. The ranked abundance pattern of this category has negative correlations ($P \leq 0.05$) with ranked temperature ($\rho = -0.69$) and salinity ($\rho = -0.68$) values (Table 9). Both the myctophid and other mesopelagic categories appear to have abundance patterns unrelated to warm-cold hydrographic conditions (Table 9).

TABLE 9.—Correlations of across-year abundance ranks of zooplankton and ichthyoplankton categories with ranked (high to low) mean temperature and salinity values from nine July–September sampling periods off northern Chile, 1964–83. Correlations based on Spearman's rho tests. Significant values at $P \leq 0.05$ are indicated, but note use of multiple testing. PL = larvae of pelagic species; OL = other larval taxa.

	Temperature (°C)		Salinity (‰)	
Zooplankton	−0.48		−0.37	
PL	−0.10		−0.17	
OL	−0.02		+0.05	
Larval diversity: (mean no. taxa/tow)	+0.12		0.00	
Myctophids	+0.02		+0.12	
Other mesopelagic taxa	+0.28		+0.12	
Coastal taxa	−0.69	$P < 0.05$	−0.68	$P = 0.05$

Zooplankton biomass values show negative but nonsignificant correlations with temperature and salinity (Table 9). This is in agreement with the time-series analysis results of Bernal et al. (1983) which demonstrated no consistent relations of zooplankton biomass with cold- or warm-water events.

Species Groups and Hydrographic Conditions

The species groups formed by similarity of between-year abundance ranks demonstrate both positive and negative correlations with cold- and warm-year conditions (Table 10). Group I and Pair II and their member species have negative correlations with ranked temperature and salinity values indicating a tendency for higher

surface temperature (°C) and salinity (‰) values during July–September available. Hydrographic "condition" descriptions for these periods are from Robles et al.

	1969	1970	1972	1973	1983
Temperature (°C)					
N	35	N.A.	110	43	24
Range	14.6–17.5		15.5–18.5	14.3–17.4	15.1–19.0
$\bar{X}$	16.0		17.2	15.8	17.2
(S)	(1.0)		(0.7)	(0.9)	(0.9)
Rank	5		1.5	6	1.5
Salinity (‰)					
N	35	N.A.	108	43	20
Range	34.60–35.19		34.75–35.96	34.60–35.13	34.81–35.39
$\bar{X}$	34.87		35.05	34.82	35.09
(S)	(0.16)		(0.18)	(0.13)	(0.19)
Rank	5		3	7	1
Hydrographic condition:	Warm	Cold	El Niño	Transition	El Niño

TABLE 10.—Correlations of across-year abundance ranks of larval fish species groups and member species with ranked (high to low) mean temperature and salinity values from nine July–September sampling periods, 1964–83. Correlations based on Spearman's rho tests. Group correlations based on ranks of summed within-year ranks of member species. Significant values at $P \leq 0.05$ are indicated but note use of multiple testing. ** = abundance ranks adjusted to accommodate for apparent large sampling depth-related catch differences.

Species	Temperature (°C)		Salinity (‰)	
Group I	−0.78	$P < 0.05$	−0.78	$P < 0.05$
Engraulis ringens	−0.52		−0.62	
Normanichthys crockeri	−0.69	$P < 0.05$	−0.72	$P < 0.05$
Blenniid D	−0.74	$P < 0.05$	−0.77	$P < 0.05$
Sebastes sp.	−0.67		−0.55	
Group II	+0.27		+0.20	
Diogenichthys laternatus	+0.45		+0.50	
Bathylagus nigrigenys	+0.27		+0.20	
Vinciguerria lucetia	+0.12		−0.14	
Pair I	+0.70	$P < 0.05$	+0.49	
Sardinops sagax	+0.69	$P < 0.05$	+0.50	
Myctophum nitidulum	+0.61		+0.35	
Pair II	−0.62		−0.57	
Lampanyctus parvicauda	−0.68	$P = 0.05$	−0.48	
*Triphoturus mexicanus***	−0.50		−0.53	

abundances during colder, lower salinity periods. The rankings of Group I (based on ranks of summed within-year member species ranks) are significantly correlated ($P < 0.05$) with both temperature and salinity ($\rho = -0.78$ in both cases). Within this group the rankings of *Normanichthys crockeri* and Blenniid D are correlated ($P < 0.05$) with temperature and salinity ($\rho = -0.69$ to -0.77); the correlation of *Sebastes* with temperature is also relatively strong ($\rho = -0.67$). Within Species Pair II, *Lampanyctus parvicauda* abundance has a relatively strong negative correlation with temperature ($\rho = -0.68$).

Group II and Pair I and their member species have positive correlations of ranked abundance with temperature and (with one exception) salinity values (Table 10) suggesting a tendency for higher abundances during warmer, higher salinity conditions. These correlations are all nonsignificant and generally weak for Group II and its member species (*Bathylagus nigrigenys*, *Vinciguerria lucetia*, and *Diogenichthys laternatus*). Pair I has a positive correlation ($P < 0.05$) with temperature ($\rho = +0.70$) primarily due to sardine abundance ranks.

Species Percentage Composition Relative to Hydrographic Conditions

Ichthyoplankton percentage composition shows no striking warm year vs. cold year related patterns. Total ichthyoplankton composition comparisons between years of "similar" hydrographic conditions do not give overall higher PSI values than do comparisons between years of different conditions (Table 11A). PSI values (ranges, means, and proportions of high and moderate values) from comparisons of cold, transition, and warm years are similar. However, highest values (91.6–94.9) come from cold vs. transition year (1970 vs. 1966 and 1973) and between-transition year (1966 vs. 1973) comparisons. Additionally, intercomparisons of the transition, warm, and El Niño years give relatively lower values than do cold-year comparisons. Comparisons between El Niño years give generally PSI low values.

TABLE 11.—Within- and between-hydrographic period ichthyoplankton composition comparisons presented as range, mean, and standard errors of percent similarity index (PSI) values and numbers (N) out of total comparisons having moderate to high (e.g., ≥65) values. A. Total larvae. B. OL (other larval taxa) fraction.

		PSI values for			
		Cold	Transition	Warm	El Niño
A. Total larvae					
Cold years	Range	67.8–82.2	62.7–94.9	62.8–82.5	7.3–79.1
(1964, 1967, 1970)	$\bar{X}$	76.6	79.4	73.0	46.5
	(SE)	(4.5)	(5.2)	(3.6)	(9.6)
	N	3/3	5/6	4/6	4/9
Transition years	Range			57.8–65.1	3.3–79.4
(1966, 1973)	$\bar{X}$		91.9	62.5	39.7
	(SE)			(1.6)	(12.9)
	N		1/1	1/4	2/6
Warm years	Range				18.8–76.4
(1968, 1969)	$\bar{X}$			79.4	52.3
	(SE)				(9.2)
	N			1/1	2/6
El Niño years	Range				22.0–45.3
(1965, 1972, 1983)	$\bar{X}$				31.9
	(SE)				(7.0)
	N				0/3
B. OL					
Cold years	Range	46.0–75.8	30.5–68.3	47.0–85.2	33.2–88.1
(1964, 1967, 1970)	$\bar{X}$	58.6	48.0	64.6	57.6
	(SE)	(8.9)	(5.7)	(5.4)	(5.9)
	N	1/3	1/6	3/6	3/9
Transition years	Range			36.8–67.9	18.5–66.2
(1966, 1973)	$\bar{X}$		37.5	51.7	41.0
	(SE)			(6.4)	(7.8)
	N		0/1	1/4	1/6
Warm years	Range				37.2–68.4
(1968, 1969)	$\bar{X}$			58.5	53.1
	(SE)				(5.2)
	N			0/1	1/6
El Niño years	Range				54.3–58.7
(1965, 1972, 1983)	$\bar{X}$				55.8
	(SE)				(1.5)
	N				0/3

The OL percentage composition similarly does not demonstrate clear hydrographically related patterns (Table 11B). As with the total larvae, comparisons of cold vs. other years yield most of the moderate to high PSI values. Highest values (88.1 and 85.2) come from comparisons of cold vs. El Niño (1965 vs. 1967) and cold vs. warm (1964 vs. 1969) years. Comparisons within and between transition, warm and El Niño years give primarily low values. Recalculation of PSIs to accommodate for *Triphoturus mexicanus* lowers mean values for comparisons with 1973 and 1983 by only 0.4–2.3 and does not affect the overall results.

Chronological Considerations of Species Composition

When the total larval and OL PSI data are considered in terms of chronological rather than hydrographic periods, various patterns become apparent (Table 12). For the total ichthyoplankton, comparisons within the 1964–69 data set and between this and the 1970–73 data set give similar means, ranges, and proportions of moderate to high values. In contrast, comparisons within the 1970–73 data set provide more similar values and a significantly higher mean value than results from comparisons within the 1964–69 set (Z test, $P < 0.01$). This suggests that, despite the varied hydrographic conditions represented during the 1970–73 period, conditions were favorable for a repeated fairly similar anchoveta-dominated ichthyoplankton assemblage during July–September months.

Chronologically grouped comparisons of the OL fraction provide somewhat different patterns from those of the total ichthyoplankton (Table 12B) and indicate a marked change in species

proportions between 1964–69 and later years. Comparisons within the 1964–69 OL data set yield all of the high and most of the moderate PSI values. The mean PSI value from these comparisons is significantly higher ($P < 0.05$) than that from 1964–69 vs. 1970–73 comparisons. As with the total larvae, the 1970–73 PSI values are similar and moderately high and the 1983 comparison values are relatively low compared with other years. Accommodation for *T. mexicanus* abundance reduces slightly (1.1–3.1) the mean values from comparisons with 1970–73 and 1983 data sets and strengthens the significance of difference ($P < 0.01$) between 1964–69 and 1964–69 vs. 1970–73 mean values.

The difference in OL PSI values between 1964–69 and 1970–83 is, to a great extent, due to abundance shifts of Group II and Pair II species. The abundance ranks of all three Group II species (Table 7) indicate significantly higher abundances during 1970–83 than in earlier years (Man Whitney U tests, all P's ≤ 0.05). Additionally, the averaged abundance estimates from these four years are significantly higher than from earlier years (Z tests; $P < 0.01$ for *Bathylagus nigrigenys* and *Vinciguerria lucetia*, $P < 0.05$ for *Diogenichthys* spp.). Together *B. nigrigenys*, *V. lucetia*, and *Diogenichthys* spp. (primarily *D. laternatus*) contributed 46.5–72.8% of the OL collected during 1970–83 compared with 5.8–37.1% during 1964–69 (Table 13).

In contrast, Pair II species *Lampanyctus parvicauda* and *Triphoturus mexicanus* were relatively less abundant during 1970–83 than in previous years. These two species contributed 21–66% of the OL during 1964–69 compared with <22% during 1970–83 (Table 13). With adjustments to *T. mexicanus* abundance these species proportions in 1973 and 1983 decrease to 11.8% and 13.2%, and those of the Group II species increase to 49.9% and 71.4%, respectively. The relative abundance decrease of Pair II was primarily

TABLE 12.—Within- and between-time period ichthyoplankton composition comparisons presented as ranges, means, and standard errors of percent similarity index (PSI) values and numbers (N) out of total comparisons having moderate to high (e.g., ≥65) values. A. Total larvae. B. OL (other larval taxa) fraction.

		PSI values for		
		1964–69	1970–73	1983
A. Total larvae				
1964–69	Range	33.9–82.5	38.2–91.9	3.3–31.0
	$\bar{X}$	67.4	67.7	18.2
	(SE)	(3.6)	(3.6)	(4.3)
	N	9/15	11/18	0/6
1970–73	Range		79.1–95.0	7.3–22.0
	$\bar{X}$		84.4	12.8
	(SE)		(5.2)	(4.7)
	N		3/3	0/3
B. OL				
1964–69	Range	29.2–88.1	26.2–67.9	18.5–54.4
	$\bar{X}$	60.2	48.4	40.7
	(SE)	(4.6)	(2.5)	(5.6)
	N	7/15	1/18	0/6
1970–73	Range		66.2–74.4	58.6–60.2
	$\bar{X}$		69.7	59.2
	(SE)		(2.4)	(0.5)
	N		3/3	0/3

TABLE 13.—Percentage contribution by dominant OL (other larval taxa) species collected during July–September sampling periods, 1964–83. Species arranged according to group affiliations based on across-year ranked abundance patterns.

	Percentage contribution for									
	1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
Group I										
Normanichthys crockeri	15.61	1.94	67.40	3.51	5.15	22.13	12.52	1.02	15.72	—
Sebastes sp.	0.36	—	0.60	0.63	1.79	—	—	—	0.35	—
Blenniid D	4.81	0.52	4.00	4.45	9.40	2.16	—	1.19	4.31	0.44
Group total	20.78	2.46	72.00	8.59	16.34	24.29	12.52	2.21	20.38	0.44
Group II										
Bathylagus nigrigenys	3.63	6.60	1.61	6.08	13.87	0.75	9.01	24.14	17.53	13.78
Vinciguerria lucetia	2.81	0.52	0.70	3.82	6.94	2.16	26.78	23.37	9.31	1.62
Diogenichthys spp.	5.63	24.45	3.50	19.11	16.33	12.15	26.78	25.29	19.68	49.96
Group total	12.07	31.57	5.81	29.01	37.14	15.06	62.57	72.80	46.52	65.36
Pair I										
Myctophum nitidulum	0.36	—	0.10	—	0.89	0.75	—	2.05	2.15	2.01
Pair II										
Lampanyctus parvicauda	37.21	41.40	15.77	39.47	24.16	32.11	7.13	12.67	6.06	6.78
Triphoturus mexicanus	28.86	20.44	4.99	18.17	10.29	26.37	14.27	8.40	11.82	14.70
Pair total	66.07	61.84	20.76	57.64	34.45	58.48	21.40	21.07	17.88	21.48

due to the increased numbers of Group II species and decreased numbers of *L. parvicauda*. The 1970–83 averaged abundance of *L. parvicauda* is significantly lower (Z test; $P < 0.01$) than that of 1964–69. *Triphoturus mexicanus* averaged abundance (both adjusted and unadjusted values) is similar ($P > 0.05$) between the two time periods.

DISCUSSION

The northern Chilean ichthyoplankton data set is obviously weakened by lack of information from the 1974–82 period; this missing information is critical for an appreciation of the temporal extent and relative constancy of the apparent ichthyoplankton composition change in 1970–73 vs. earlier years. This data set also suffers from limited seasonal coverage which prohibits examination of between-year variations in spawning time and intensity as a cause of interannual abundance fluctuations and apparent composition change. However, the existing data set does provide coherent coverage over varied hydrographic conditions between 1964 and 1973 and is sufficient to test for correlations with short-term (e.g., year to year) fluctuations in hydrographic conditions.

The large interannual changes in abundance and composition of the northern Chilean ichthyoplankton can to a certain extent be related to interannual changes of hydrographic conditions in the Humboldt Current. This has been demonstrated through correlations of ranked temperature and salinity values and abundances of coastal species, sardine, and *Lampanyctus parvicauda* (Tables 9, 10). The temperature and salinity values used in these correlation tests represent ambient conditions during the July–September spawning period and therefore possibly reflect only conditions affecting egg and early larval (e.g., to stages capable of substantial net avoidance) survival. These values do not necessarily reflect longer term conditions affecting abundance, distributions, and fecundities of adult populations or later larval survival and recruitment. However, there is a generally good correspondence between these values and reported longer term hydrographic conditions in the Humboldt Current over the 19-yr timespan (e.g., Table 8; Robles et al. 1976; Bernal et al. 1983; Guillén 1983; Bakun 1987).

Despite significant correlations between abundances of some ichthyoplankton components and temperature and salinity values, there is no apparent consistency of total larval or OL species percentage compositions during years of "similar" hydrographic conditions (Table 11). More coherent patterns emerge from considerations of the 1964–69 and 1970–73 data sets (Table 12). This chronological separation is also supported by the ranked abundance patterns of the various species groups and pairs (Table 7).

Among the least confusing across-year abundance patterns demonstrated by the ichthyoplankton are 1) generally greater abundance of Group II species after 1969, 2) greatest abundance of Pair I species after 1970, and 3) predominantly higher abundances of one of the Pair II species prior to 1970 (Table 7). Associated with the Group II and Pair II abundance patterns are large shifts in their relative proportions (Table 13).

The shift from relatively large percentage contributions by *Lampanyctus parvicauda* and *Triphoturus mexicanus* to larger proportions of *Diogenichthys* spp., *Bathylagus nigrigenys*, and *Vinciguerria lucetia* after 1969 is notable. The abundances of these mesopelagic species, unlike those of anchoveta and sardine, are not directly influenced by man's fishing activities and so may be interpreted as indicators of environmental change. Furthermore, the timing of these species absolute and relative abundance changes preceded by several years the dramatic changes in anchoveta and sardine stocks off of northern Chile (Fig. 4) and so cannot be directly related to biological consequences of change in the dominant pelagic schooling fish stocks.

Although fragmentary, there is evidence for a change in zooplankton biomass values off northern Chile (18°–24°S) occurring in 1969 (Fig. 5) which, like OL percentage composition, suggests a possible environmental change. Time series analysis of quarterly zooplankton biomass values during 1964–73 indicate generally lower biomass during 1969–73 relative to the 1964–68 period. As with total larval abundance (Table 9), these zooplankton biomass variations do not appear to be related to warm year-cold year events (Bernal et al. 1983).

The changes in OL composition and zooplankton biomass suggest that there was subtle but large-scale (low-frequency) environmental transition occurring in the 1969–70 period. Various indications of environmental change occurring about this time are present in long-term physical data bases from Chile and Peru. Predominantly

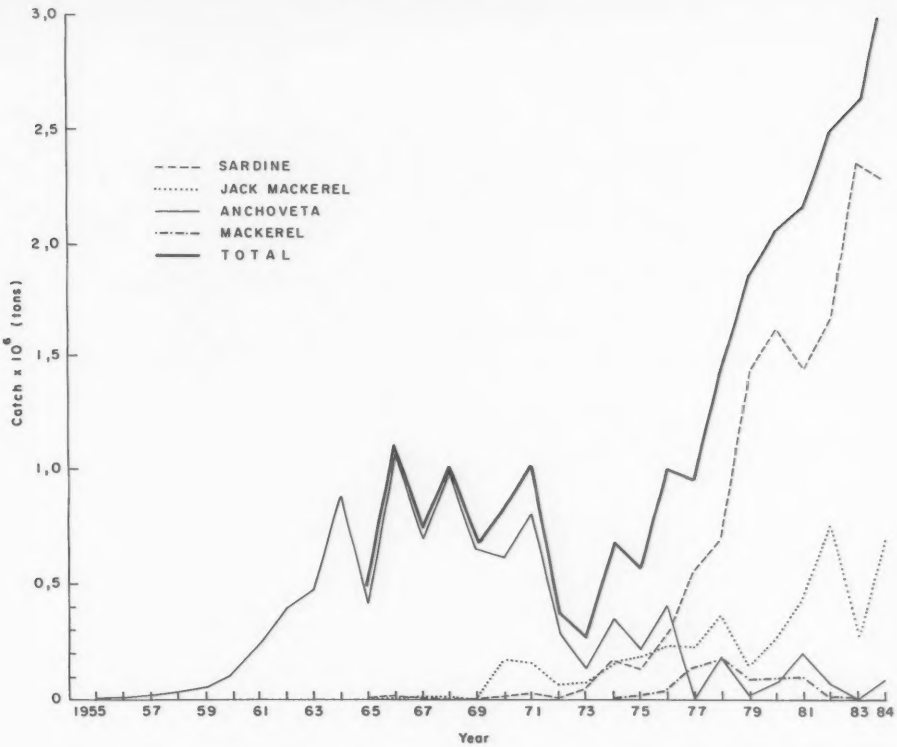

FIGURE 4.—Total catch and catch of dominant species taken in the northern Chilean pelagic fishery, 1955–84.

negative sea surface atmospheric pressure anomalies occurred off of Arica from 1960 to 1972 with a strong negative anomaly occurring in 1969; predominantly positive anomalies occurred there after 1972 (Fig. 6A). A similar but less extreme change from negative or neutral anomalies to predominantly positive anomalies occurred off Iquique (20°S) in 1970 (Fig. 6B; Kelly and Blanco 1983).

Off Peru (5°–15°S) the wind driven turbulent mixing index of surface waters shows a general increase during and after the 1972 El Niño event (Fig. 7A; Bakun 1987). A probable result of this increased turbulence is an increase in standard deviations associated with monthly temperature values; standard deviations above the 30-yr mean generally persisted throughout the year from 1972 to 1984 (Fig. 7B) and suggest increased physical variability and heterogeneity in this later period. Comparable data sets from northern Chile are not available to determine if these latter two features were also characteristic of the Chilean area.

How these observed atmospherically related changes could be related to changes in the marine environment off northern Chile is uncertain. It is possible that the observed changes in atmospheric pressure off Arica and Iquique have associated changes in advection of water mass and faunal sources. Bernal et al. (1983) discussed El Niño related changes in water mass distribution off Chile in 1972 and 1973 relative to cold-year 1967. These changes involved southerly extensions of oceanic subtropical and equatorial subsurface waters, strengthening of the spring-summer thermocline, and cessation of coastal upwelling. These authors did not examine water mass distributions in the 1968–70 period. However, lowered zooplankton biomass starting in 1969 and the OL composition change starting around 1970 suggest that the hydrographic conditions attributed to the 1972 El Niño may have been an intensification of

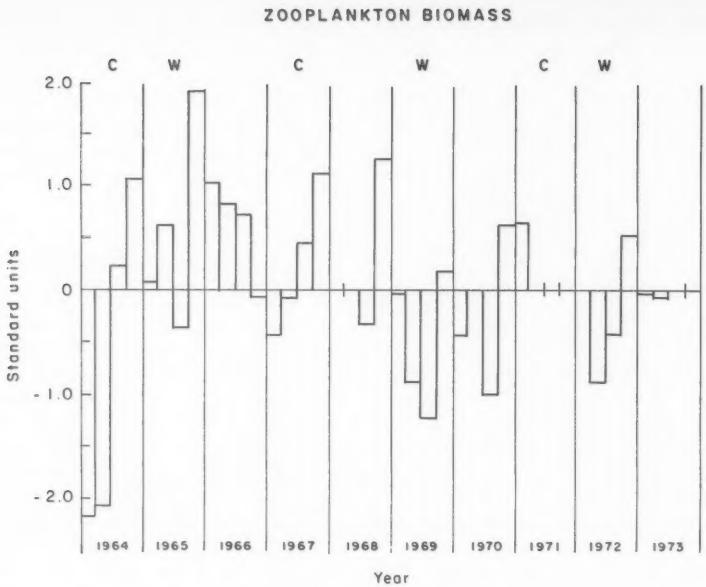

FIGURE 5.—Time series estimates of quarterly zooplankton biomass values from northern Chile (18°–24°S), 1964–73, standardized according to the long term standard deviation. W = warm years; C = cold years. From Bernal et al. 1983.

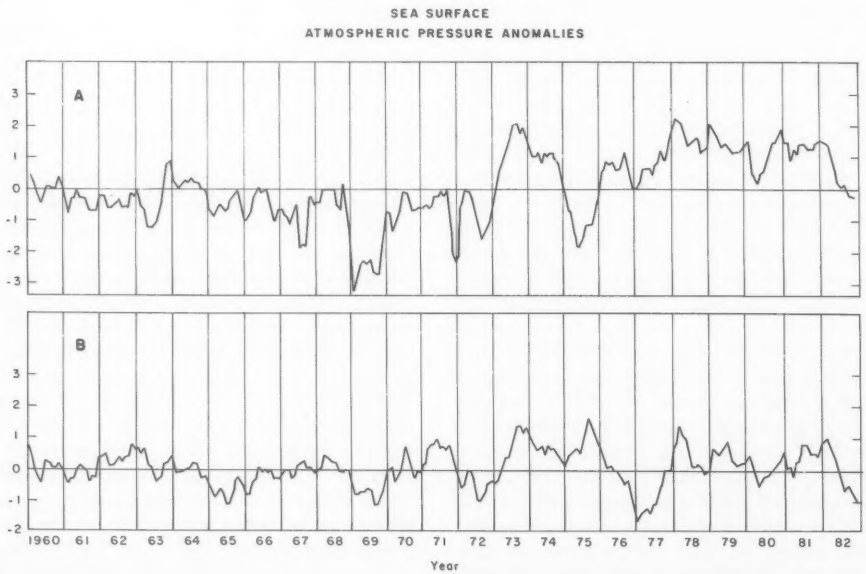

FIGURE 6.—Sea surface atmospheric pressure anomalies off of (A) Arica (18°S) and (B) Iquique (20°S), 1960–82. From Kelly and Blanco 1983.

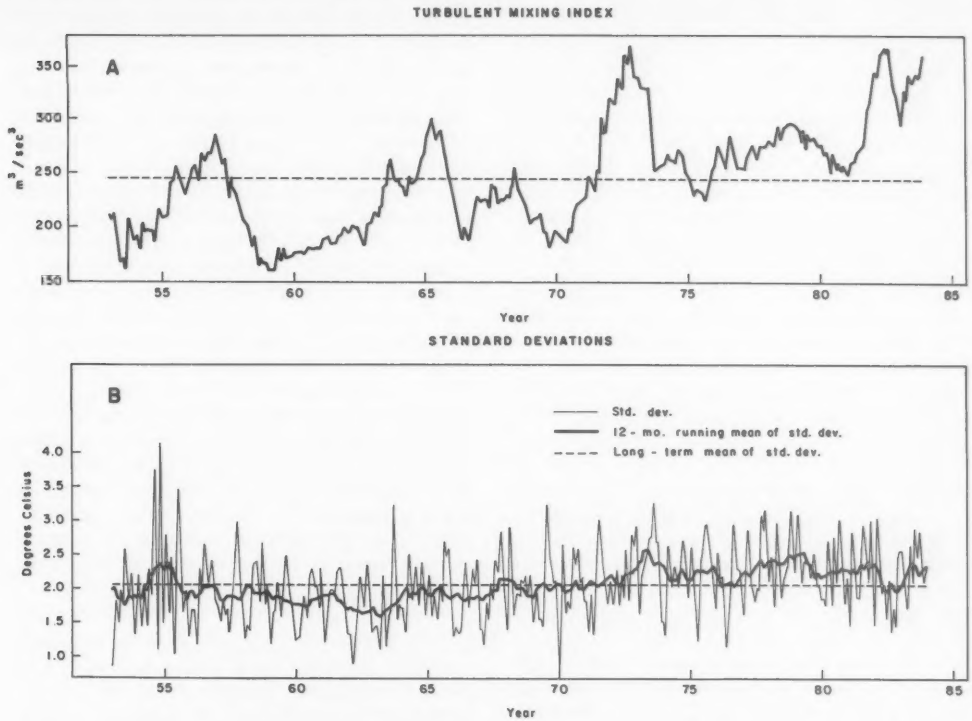

FIGURE 7.—(A) Surface layer turbulent mixing index values and (B) standard deviations and 12-mo running mean of standard deviations associated with mean monthly sea surface temperature values off of Peru (5°–15°S), 1953–84. Dotted lines represent long-term mean values of each index. From Bakun 1987.

conditions initiated during the warm 1968–69 period; these could possibly have persisted and intensified again during the 1976 and 1983 El Niño events.

It is also likely that the 1970 change in OL composition is related to onshore advection of northern or oceanic water masses and associated faunal assemblages, but this cannot be confirmed. All involved species are relatively abundant in coastal Peruvian and south eastern tropical Pacific waters (Ahlstrom 1971, 1972; de Castillo 1979; Santander and de Castillo 1979) and in more southern coastal Chilean waters (Table 2), but their wintertime relative abundances in these areas have not been documented. It is also possible that the changes in species composition are related to locally lowered zooplankton abundance (e.g., that the Group II species are relatively more successful than *Lampanyctus parvicauda* and *Triphoturus mexicanus* during periods of lowered secondary productivity levels). Alternatively, the observed change could be due to altered seasonal spawning activity which is not treated in the present study. However, whatever the cause, there is evidence for an environmental change in the study area, and this may be also implicated in changes occurring within the PL ichthyoplankton fraction.

Increased abundances of sardine and *Myctophum nitidulum* (Pair I species) during and after 1972 may be further evidence for a changed marine environment off of northern Chile. Additionally, the significant correlation between larval sardine abundance and temperature (Table 10) suggests that elevated temperatures may have been important for increased spawning activity and/or increased success of hatching and early larval survival. Given this observation one may speculate that the increased sardine catches after 1973 (Fig. 4) are related to increased frequency of warm-water events in the 1964–84 period relative to earlier years. Increased sardine

catches in 1973 resulted from apparently extremely good survival and recruitment of individuals spawned during the warm 1968–69 period (Serra[3]). Similarly, good survival of the large 1972 El Niño spawn could explain the huge catch increases in 1976 and later years (Fig. 4). However, mean biomass estimates of age groups contributing to the Chilean fisheries catch from 1974 to 1981 (Serra 1983) indicate increasing contributions after the 1967 year class with marked increases beginning with the 1970 year class; this suggests that factors other than temperature (e.g., environmental change starting in 1969–70) may also be responsible for increased larval survival and recruitment. A possible cause is increased nearshore influence of equatorial and subtropical waters (Santander and Flores 1983). Because the sardine abundance increase was initiated prior to the 1972 anchoveta decline off northern Chile (Fig. 4), it is difficult to implicate reduced anchoveta competition as the cause of the early sardine population growth in this area.

The grouping of anchoveta with three coastal species (Group I), and significant correlation of anchoveta and *Normanichthys crockeri* larval abundances are extremely interesting and imply that the spawning intensity and/or early stage survival of these four species are influenced in similar ways by interannual changes off northern Chile. Unfortunately, little is known about the natural histories or population abundances of the coastal species. Because of the group composition, it is logical to suspect that coastal processes are important factors influencing their larval abundance. The significant negative correlation of the group as a whole, and of two of the coastal species, with ranked temperature and salinity values (Table 10), suggests that coastal upwelling and/or increased coastal influence by subantarctic waters, and theoretically enhanced food supplies, are important factors.

Given the present data set and information from recent publications, a case can be made for a low-frequency environmental change influencing the abundances of anchoveta and sardine larvae as well as the larvae of coastal and mesopelagic species during the 1964–84 period. The Chilean OL composition suggests an environmental change (e.g., an atmospherically related oceanic circulation change) starting with the 1968–69 warm-water event. This coincided with apparent successful survival of sardine larvae and markedly increased recruitment by 1968 and later year classes despite varied warm water-cold water events between 1968 and 1973. Physiological anomalies of Peruvian anchoveta stocks in 1971 suggest that these fishes may have experienced environmental change at that time. Unusually low proportions (e.g., 40% vs. typically 90%) of potential spawning-sized fish were sexually mature during the 1971 spawning season and fat content of the 1971–72 catch was anomolously high, indicating unusually low transfer of body fat to gonadal products (Sharp 1980). Starting with the 1972 El Niño was 1) an obvious increased incidence of penetration of subtropical surface waters toward the Peruvian coast, 2) coincidental onshore and southward expansion of sardine spawning activity off both Peru and Chile, 3) southward expansion of Peruvian anchoveta spawning activity into new spawning areas between 14°S and 18°S (e.g., to northern Chile), and 4) a succession of years of poor anchoveta larval survival off Peru and Chile (Santander and Flores 1983; Serra 1983). Environmental conditions favorable for growth of sardine populations, as well as of mackerel and jack mackerel populations, off both Chile and Peru have persisted since the early to mid-1970's (Santander and Flores 1983; Serra 1983).

The lack of Chilean ichthyoplankton data from the 1974–82 period precludes evaluation of the constancy of altered species composition during that time. However, there are indications that change is once more occurring off northern Chile. Preliminary analysis of ichthyoplankton samples collected between Arica and Antofagasta during 4–14 August 1985 indicates a clear dominance by anchoveta larvae at a markedly higher mean abundance level than encountered in the 1964–83 samples; sardine and *Trachurus* larval abundances are comparable to those in the 1973 samples (Table 14). The other species have not yet been analyzed, but *Normanichthys crockeri* is

TABLE 14.—Mean abundance estimates and standard errors (numbers per 10 m²) and percent frequency of occurrence (F) of PL taxa, OL and total larvae collected in 81 100–0 m WP_2 net samples off northern Chile (18°–24°S) during 4–24 August 1985.

Species	$\bar{X}$	(SE)	(F)
Engraulis ringens	5,535.3	(1,844.1)	(90.4)
Sardinops sagax	63.8	(24.9)	(26.6)
Trachurus murphyi	1.2	(0.9)	(2.1)
Other species	233.7	(28.4)	(92.5)
Total	5,834.0	(1,838.2)	

[3]Serra, R. Unpubl. manuscr. Subsecretaria de Pesca, Teatinos 120, Piso 11, Of. 44, Santiago, Chile.

once again noted to be among the abundant OL taxa. It will be of great interest to see the recruitment resulting from this 1985 anchoveta spawn. If the 1985 anchoveta year class is relatively successful during this period of continued large sardine stocks, it will lend support to the idea that the anchoveta-sardine population fluctuations have been primarily regulated by low-frequency hydrographic events. In a long-term context such events may not be unusual to the Humboldt Current area. Fish scales present in sediment records from coastal Peruvian waters indicate that sardine replacements of typically dominant anchoveta stocks have occurred at infrequent intervals over the past 11,000 years (De Vries and Pearcy 1982). In light of this, the ecological events of the past 20 years may be naturally occurring, physically mediated, but probably fisheries enhanced, fluctuations in this hydrographically complex region. Because of our limited time reference, we have not previously acknowledged such fluctuations as being "normal".

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ESTIMATION OF NATURAL MORTALITY IN FISH STOCKS: A REVIEW

E. F. VETTER[1]

ABSTRACT

The instantaneous rate of natural mortality (M) is an important but poorly quantified parameter in most mathematical models of fish stock dynamics. This report reviews methods used commonly to estimate M for fish stocks, sensitivity of some common fishery models to values chosen for M, and evidence refuting the common assumption that a constant value can be an adequate approximation of M within single stocks.

With the exception of simple surplus production models (e.g., Schaefer 1954; Pella and Tomlinson 1969) all mathematical models of fish stock dynamics include as a parameter the instantaneous rate of natural mortality (M). The models do not require explicitly any particular form for M; it can be constant or can vary in any imaginable form. But because natural mortality has proved extremely difficult to measure directly, M is assumed almost universally to be some constant specific to whatever stock is being modeled. This is particularly true for analyses of commercial fish stocks, which often require estimates of M only for the postrecruit ages. Decreases in natural mortality with increasing age during egg and postlarval stages are so dramatic compared to apparent changes during postrecruitment ages (e.g., Cushing 1975) or compared to differences between different sexes, collection sites, seasons, years, cohorts, or stocks within species, that variations in M during these later (postrecruitment) ages are often assumed negligible.

Whether this assumption is in fact acceptable is the subject of this report. The answer is no, it is probably not acceptable in most cases. That answer follows from the information presented in Sections II through V, with the following conclusions:

Section II: Current methods for estimating natural mortality: a review of methods used currently to estimate M in fish populations. All of these methods have strong limitations or disadvantages.

Section III: Sensitivity of fishery models to choices for M: a review of the sensitivity of some standard fishery models to different choices for input value(s) of M. Existing studies show that the models are sensitive and that sensitivity is affected not only by the values chosen for M, but also by interactions between M and the values chosen for other parameters in the models.

Section IV: Evidence for nonconstant M; factors influencing death rate: a review of factors assumed or shown to affect M in fish stocks. Available information implies that many such factors exist, acting alone or in concert.

Section V: Evidence for nonconstant M; variability within and between groups: a review of existing quantitative evidence for the extent of variability in M between but especially *within* stocks. Because almost all fishery models focus on single stocks, variability within stocks (as opposed to between stocks) is the most important question. Some studies show strong differences between mortality rates of various groups of fish; some do not. Those which do not have tended to assume there would be none, and have often used catch curve regression analysis to derive a single estimate from data combined over many groups (usually years) of data. The few studies from which it is possible to determine ranges of estimates show differences of at least 50 to 100% between minimum and maximum estimates for single groups (e.g., stocks) of fish.

The report's major conlcusions are that natural mortality is far from constant for many fish stocks, and that this variability is extensive enough that it should not be ignored. Analyses of

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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fish stock dynamics need much more rigorous estimates of **within-stock** variability (both trends and variance) in M for exploited fish stocks.

II. CURRENT METHODS FOR ESTIMATING NATURAL MORTALITY

Three methods are used currently or have been proposed to estimate M in fish populations: 1) analysis of catch data, usually from commercial fisheries but also from sampling programs specifically conducted for stock assessment (this includes mark-recapture studies), 2) correlations of M with other life history parameters, and 3) estimation of deaths due to predation. I describe below each method in turn, listing both advantages and disadvantages of each.

Catch-Analysis Methods

Methods for deriving estimates of natural mortality from catch data are based on measuring decreases in abundance, either relative or absolute, in groups of fish during two or more successive periods of time. Groups may be distinguished on the basis of any identifiable characteristic, e.g., size (length or weight), age, sex, location and time of capture, or some identifiable tag or mark.

The most common grouping is by age, for two reasons. First, age has been considered historically the most important factor potentially affecting estimates of mortality rate and subsequent results from the most commonly used fishery models (e.g., Heincke 1913; Baranov 1918). This is probably because the methods were developed for temperate water fisheries which tend to have obvious annual reproductive cycles, so that individual year classes are often relatively easy to distinguish. Second, the earliest method of estimating M (catch curve analysis, discussed below) depends on determining the rate during successive ages.

Regardless of the grouping criterion, methods for estimating M use generally one of two types of data. The first type is simply subsamples of unmarked catch. These subsamples contain fish selected randomly and classified into groups on the basis of size (length or weight). The second type is mark-recaptures, in which previously marked individual fish can be identified and classified after recapture into groups on the basis of this positive identification. Estimates of mortality are usually derived from samples of unmarked fish by analysis of resulting "catch curves" (Ricker 1975). Because it has been used so frequently, catch curve analysis is discussed below in some detail.

With marking it is possible to follow the history of individual fish, so many different types of estimation procedures exist for deriving estimates of mortality from mark-recapture data (e.g., Ricker 1975; Jones 1979; Brownie et al. 1985). Because so many variations are possible, marking experiments are discussed only generally, stressing the basic advantages and disadvantages of marking data relative to data from unmarked samples, in deriving estimates of mortality from these data.

Size-frequency distributions from unmarked subsamples of catch (the first type of data) are converted usually to age-frequency distributions, on the basis of previously determined relationships between age and length or age and weight. Subsequent analyses concentrate on analyzing this resulting curve of age-composition (e.g., Ricker 1975). Abundance usually decreases exponentially with size (or age) in this type of sample. Converting the abundances to their logarithmic values often results in a relatively linear decrease during most exploited ages (or sizes), after some initial increase in vulnerability. Graphs of these logged-frequency distributions are usually called "catch curves", and their analysis, "catch curve analysis". "Catch curve analysis" generally consists of determining the best-fit straight line through the decreasing portion of the logged-frequency distribution, because if the decrease in abundance is truly exponential, the slope of this line through the log-transformed data is the instantaneous rate of decrease in abundance (e.g., Ricker 1975).

There are two basic types of catch curves, distinguished on the basis of when the data were collected and how many groups are represented in the curves. The first, horizontal catch curves, includes data from several groups (e.g., size or age classes) collected at a single point in time (or combined from two or more points in time). Thus, horizontal catch curves reflect "ancient history". The individuals contributing to the frequency distribution were not originally all members of the same group. To use this type of catch curve, one must assume that for each successive age, risk of mortality has been historically the same for all individuals achieving that age. If this has not been the case, the catch curves may show various types of curvature in the descending leg, but absence of curvature is no guarantee that the rates have in fact been constant.

Thus, horizontal curves are subject to the extremely restrictive assumption that the groups from which the data were collected must be in steady state relative to each other, i.e., their relative abundances must be constant through time. If this is true, then a graph of data collected at a single point in time, which may include, for example, individuals from 5 consecutive year classes displayed as frequencies at 5 consecutive ages, will look the same as the 5 graphs of data that will result from collecting samples during 5 consecutive years (ages) from each of the 5 year classes. If these conditions are not met, simple linear fitting to determine a single estimate for mortality will be inappropriate.

The second type of catch curve, longitudinal, includes data collected from a single identifiable group over a protracted period of time. Most often, this will be a single cohort of fish such as single year class, sampled during successive years. Longitudinal curves are not subject to the assumption of steady state, but do share with horizontal catch curves several other severe disadvantages. These include 1) groups must be adequately identifiable; 2) groups must be closed to migration, so that changes in abundance are due only to fishing or natural mortality, or if migration does occur, it must occur in proportion to the age distributions in the local groups; 3) samples must represent adequately the true composition of the groups in nature; 4) rate(s) of mortality must be relatively constant between groups over time, so that the log-transformed frequency distributions are truly linear (e.g., Jensen 1984); 5) compensatory relationships between stock levels and natural mortality, or fishing mortality and natural mortality, must not be present.

Methods for estimating M, which assume to greater or lesser degrees that the conditions listed above are met, have been described repeatedly. The methods tend to fall into two categories. Methods in the first category estimate M from catch records of unexploited or lightly exploited groups of fish. In these groups, F equals or approximates zero. Therefore, the observed rate of decrease (Z) equals or approximates M, because Z equals the sum of F and M (e.g., Heincke 1913; Baranov 1918; Ricker 1947; Beverton and Holt 1957; Robson and Chapman 1961; Pauly 1982; Munro 1982; and among others).

Methods in the second category estimate M by determining Z at various levels of fishing effort, then using the observed relationship between Z and effort to predict, via regression analysis or manipulation of various ratios, the value of Z at zero effort (e.g., Silliman 1943; Beverton and Holt 1957; Paloheimo 1961; Lander 1962; Chapman and Murphy 1965; Paulik and Robson 1969; Gulland 1983; Butler and MacDonald 1979; Fournier and Archibald 1982; Caddy 1984; and others).

These methods are most appropriate for analyzing catches of unmarked fish. Accurate results depend strongly on accurate measures of catch per unit effort (CPUE) and constant catchability (q) because if these conditions (in addition to those listed above) are not met, observed relationships between abundances in different sample groups may not reflect true differences between groups in situ.

Marked fish present fewer problems. Advantages include 1) concentration on measuring relative rather than absolute differences between abundances of different groups, 2) immigration need not be considered, as entire original groups are known to carry marks, and 3) with sufficiently large samples, it becomes possible to test for differences in mortality rate between different groups (e.g., between ages, between sexes, or between sampling sites), rather than having to assume that such effects are negligible.

Reviews and descriptions of various mark-recapture methods appear in papers by Seber (1973), Ricker (1975), Jones (1979), and Brownie et al. (1985). Some of the newer types of marking analyses can solve many of the most vexing problems associated with traditional catch curve analysis (e.g., Reed and Davies 1980; Hochbaum and Walters 1984; Burnham and Andersen 1984; Burnham et al. 1984; Brownie et al. 1985).

Several disadvantages unique to marking operations counteract these advantages, however, even with the newer methods. These disadvantages include various types of mark-induced effects on mortality rates, behavior, and vulnerability to capture, as well as mark loss, unrepresentative mixing of marked fish with their original groups prior to recapture (e.g., Ricker 1975), and especially in commercial fisheries, underreporting or incorrect reporting of recaptures.

Both analysis of catch curves from unmarked fish and analysis of mark-recapture data have the advantage of requiring only catch (and usually effort) data, and these data can generally be collected by sampling catches from commercial fisheries. However, in addition to problems specific to each method, they have in common one or more other major disadvantages: 1) inability to distin-

guish between losses (or gains) from migration or recruitment versus losses due to fishing or natural causes, 2) imprecision in the estimates of M obtained (e.g., Beverton and Holt 1957; Taylor 1958; Bishop 1959; Paloheimo and Dickie 1966; Ricker 1975, 1977; Doubleday 1976; Pauly 1980; Larkin and Gazey 1982; Paloheimo 1980, 1982; Myers and Doyle 1983; Roff 1984), 3) sensitivity to size-specific mortality affecting the estimated age-structure of the group (Ricker 1969), 4) errors in estimates of age, such that abundances-at-age derived from age-length conversions are unrepresentative, 5) where analyses are conducted on data combined over two or more cohorts, the unlikely condition that mortality rates were in fact similar for all cohorts, and 6) problems inherent in the analyses themselves (e.g., Barlow 1984). Disadvantages 1, 4, and 5 may not apply to marked fish. Disadvantage 5 does not apply to single cohorts. But collections from marked groups and single cohorts are still vulnerable to the other problems.

Further, although in principle it would be possible to estimate M for different ages, times, or places, most commonly in practice a single, fishery-wide constant M is estimated by pooling data from throughout the fishery. By implication, the analyst is assuming that the exploited stock was more or less in steady-state over all times and areas of catch so that M was relatively constant while that data set was collected and while (historically) the observed age-distributions were being created. In fact, substantial evidence exists that M is not constant, either within a single stock over time (age) or between stocks of a given species in different areas (Sections IV and V).

A final disadvantage is that catch-curve analyses are fundamentally unmechanistic, generated simply by charting changes in abundance. Catch-curve analyses cannot predict the effect of changes in factors that control M; thus there is little hope of predicting M in the future should conditions change.

Life History Methods

A second approach to estimating the instantaneous rate of natural mortality in fish stocks is based on the observation that M often correlates strongly with life history parameters, such as growth rate, age at sexual maturity, costs of reproduction, and maximum age (Table 1).

Typically in such studies, analytical formulas are derived from theoretical relationships between the various parameters (e.g., Beverton 1964), or empirical formulas are derived from regression of M against one or more of the parameters (e.g., Hoenig 1983). These models have two significant advantages: 1) they require minimal amounts of data, and 2) they are useful in demonstrating broad trends across species and in developing ecological theory. But because they produce only a single and often very imprecise estimate of M for any given group of fish, they are not particularly effective for generating precise estimates of natural mortality or for determining the existence or extent of trends and variability in M for given stocks. They will also be no better than the methods used to estimate the values of M used in the regressions.

TABLE 1.—Studies relating instantaneous rate of natural mortality to life history traits in fish.

Traits	Species	Source
[1]T_{max}, [2]k, [3]L_{inf}, metabolic rate, reproduction	Various	Beverton and Holt 1959
T_{max}, k, L_{inf}, [4]L_{asm}, fishing	clupeids, engraulids	Beverton 1963
[5]W_{inf}	general	Ursin 1967
T_{max}, [6]$T_{max.biomass}$, k,	general	Alverson and Carney 1975
growth rate	young fish	Ware 1975
L_{asm}, gonad size, condition factor	gadoids	Jones and Johnston 1977
T_{max}	general	Blinov 1977
gonad/body weight index, [7]ASM, T_{max}, L_{inf}	general	Gunderson 1980
W_{inf}, L_{inf}, k, water temperature	175 stocks	Pauly 1980
energy cost of reproduction	general	Myers and Doyle 1983
T_{max}	various	Hoenig 1983
weight	various	Peterson and Wroblewski 1983
k, L_{inf}, L_{asm}	various	Roff 1986

[1]Maximum age,
[2]Von Bertalanffy growth parameter.
[3]Maximum length.
[4]Length at age of sexual maturity.
[5]Maximum weight.
[6]Age at occurrence of cohort's max biomass.
[7]Age of sexual maturity.

Predation Methods

A third class of estimators extends single species cohort analysis to a multispecies assemblage incorporating the major predators and alternative prey of the stock in question. Single species cohort analysis is used to estimate population abundances and annual values for the instantaneous rate of fishing mortality (F) for single groups, usually year classes, of fish (e.g., Pope 1972; Ricker 1975; Gulland 1983). The multispecies extension simply combines cohort analyses for several species (e.g., Anderson and Ursin 1977). The methods all generate estimates of M as the sum of some constant rate of nonpredatory, nonfishing mortality plus the total estimated flux of prey (stock) to each of the major predators. This feeding flux to predators is estimated by first using cohort analyses to reconstruct population sizes of the various groups of predator and prey, then combining these population sizes with observed growth rates for the predators and with estimated preferences for various prey. Thus it becomes possible to estimate the predatory component of M.

Versions of the method have been described by Anderson and Ursin (1977), Majkowski (1981), and Pope and Knights (1982). Applications in a marine system (North Sea) have been described by Anderson and Ursin (1977), in an ecosystem context, by Laevastu et al. (1982) and in lake systems by Forney (1977) and Stein et al. (1981).

The predation method has been developed primarily from analyses of marine systems, especially the North Sea, and much of the literature exists only as "mimeos" or notes associated with ICES (International Council for the Exploration of the Seas) activities. The most readily available discussion of this approach appeared in Mercer (1982), which includes a critical review and discussion by Ursin (1982) of the various methods. Several other discussions appear in Pauly and Murphy's (1982) volume of collected papers from a symposium on theory and management of tropical fisheries. Most of these papers specifically address tropical multispecies systems, but the concepts are broadly applicable. References to other, often less accessible, works can be found in these two general references.

The predation method is elegant in concept but often difficult to apply. Studies by Forney (1977) and Stein (1981) had the distinct advantages of limited species numbers in a small system, and direct quantification of stomach contents. Yet even in lake systems, the sampling problems of estimating Z, population abundances, and so forth, remain often as intractable as in large marine systems. The two greatest problems are 1) the difficulty in defining vulnerability and preference functions for the various prey stocks (e.g., Ursin 1982) and 2) the need to include cohort analyses of all the major interacting species, some or many of which may not be available commercially (and for which therefore data will be scarce).

Despite these problems the approach can certainly generate, for stocks that suffer heavy predatory mortality from other fished stocks, more realistic estimates of M than approaches that simply generate a globally fixed and invariant M. More importantly (and in contrast to the age-frequency or life history methods) the predation method has the advantage of being mechanistic. Predation-related causes and consequences of age, size, site, stock, geographic, or time trends in M can be investigated via perturbation and sensitivity analysis in computer simulation studies or, alternatively, investigated through analysis of existing catch data. It becomes possible (not necessarily feasible) to investigate the implications of varying age or abundance structures of interacting fishery resources.

Thus the predation approach has considerable conceptual appeal for fairly simple systems in which 1) predation is the major force controlling prey abundance, 2) predators have few alternative prey, 3) the possibility can be ignored that predators prefer moribund prey which were about to die anyway, and 4) all major species of predator and prey are sought commercially so that data on abundances and feeding preferences are or can be made available.

Unfortunately, the number of systems satisfying these requirements appears to be fairly small, and of course where predation is a relatively small fraction of M, the multispecies predation method will be particularly ineffective.

III. SENSITIVITY OF FISHERY MODELS TO CHOICES FOR M

Although catch-analysis, life history, and predation methods all exist currently for estimating M in fish stocks, in practice the only method used extensively is the first—direct estimation of M from analysis of catch structure. Thus the discussion below of model sensitivity to M is based on this type of estimate. The conclusions reached are

not specific to this one method. Model sensitivity to a given derived value of M will be the same, regardless of the method used to derive the value.

General Patterns

Sensitivity analyses of M in fishery models have evolved through two phases. Earlier studies noted the influence of M on estimates of maximum yield (Y_{max}) or maximum yield per recruit ($(Y/R)_{max}$), and on F_{max} (the fishing pressure required to produce maximum yield) in Beverton-Holt yield models (Beverton and Holt 1957; Hennemuth 1961; Francis 1974; Parks 1977; Bartoo and Coan 1979; Bulgakova and Efimov 1982). More recently, as cohort analyses have become more popular, more attention has been directed toward assessing the influence of M on age-specific estimates of stock sizes (N_i) and fishing mortalities (F_i) produced by these models (Murphy 1965; Pope 1971; Ricker 1971; Agger et al. 1973; Doubleday 1976; Ulltang 1977; Doubleday and Beacham 1982; Pope and Shepard 1982; Sims 1982a, 1982b, 1984). A few other studies have investigated the effect of M on estimates of maximum sustainable yield (MSY) or total biomass (Francis 1976; Deriso 1982; Beddington and Cooke 1983; Tyler et al. 1985).

Most of these studies have used a single, invariant value for M. Model sensitivity is then assessed by comparing model results using some "best" estimate of M, to results using one (or rarely, more) pair(s) of M values some arbitrary percentage above and below the best estimate. Only a few studies exist of the effects of nonconstant M, where M varies in different groups of fish **within** a given stock. These include Beverton and Holt's (1957) example of density-dependent M in plaice, and several investigations of age-specific M (Parks 1977; Ulltang 1977; Bartoo and Coan 1979; Sandland 1982; Bulgakova and Efimov 1982; Caddy 1984; Tyler et al. 1985).

No study to date has specifically addressed the problems of estimating values of M for a full fishery analysis, leading from cohort analyses (using M to estimate F_i, N_i, and recruitment R) to estimates of yield or yield-per-recruit using the same M(s) and R subsequently in the Beverton-Holt formulas. Also, no study to date has addressed the possibility and consequences of differing patterns of variability in M, although it has been suggested in one case (Ulltang 1977) that random variations will be unimportant if the rate is constant (on average) over the fished ages.

In general, the earlier analyses with yield models assuming a constant M show that *higher* estimates of M lead to 1) **lower** estimates of Y_{max} or $(Y/R)_{max}$ (because fewer survive to be caught), 2) *higher* estimates of F_{max} (you must fish a bit harder to catch a given amount of those left), and 3) **lower** estimates of age at first capture (t_c; because it pays to catch them before they die, rather than waiting for them to grow bigger but less abundant).

Including density-dependence tends to exaggerate these trends, at least for plaice in the North Sea (Beverton and Holt 1957). Including age-structured M in yield models also affects the estimates, but not necessarily in a straightforward manner. As described below in the section on numeric results, change in model output for a given change in M depends not just on the values chosen for M, but also on those chosen for the other parameters. M is not an independent parameter in these models.

Analyses with cohort or virtual population models which assume a constant value for M show that in general the effect of increasing M is to increase estimates of N_i (because the higher M is, the more fish died in addition to those being caught) and to decrease estimates of F_i. The data show only Z, which is the sum of M and F_i. Assuming Z has been constant, a decrease in F_i requires an increase in M. If Z has been variable, the lower F_i may be explained on the basis of higher N_i, a smaller proportion of which (F_i) would account for the observed catch.

The actual effect, particularly on estimates of N_i, is not necessarily that simple. As with yield models, a given change in M does not always produce the same change in model output. The result depends also on values chosen for other parameters; M is not an independent parameter.

In cohort analysis the results (estimates of N_i and F_i) are particularly sensitive to the relative sizes of F and M (i.e., to the exploitation ratio $E = F/(F + M)$). The effect of assuming an incorrect value (or series of values) of M tends to build up as the analysis proceeds backward in time. This is because with every time step backward the catch (C_i) is inflated by the factor M in order to estimate at that time the size of the entire stock, not just the size of the catch. That is

$$N_i = N_{i+1} + C_i(F_i + M)/F_i \qquad (1)$$

where F_i satisfies the catch equation

$$C_i = N_{i+1}\,(F_i/F_i + M)\,(e^{(F_i+M)\,t} - 1) \qquad (2)$$

If M is large relative to F (i.e., the exploitation ratio is low), then errors in N_i can increase progressively and become quite large at the younger ages (e.g., Agger et al. 1973; Murphy 1965; Ulltang 1977; Sims 1982a, 1982b, 1984).

Numeric Results

Although general responses of various models can be determined simply by inspection of the analytic models themselves, the quantitative change to expect in the result (output) for a quantified *change* in M (input) is not always immediately obvious. This is because M tends to occur more than once in various formulas. For example, M appears in both the numerator and denominator in the solution to the Beverton-Holt yield equation (Ricker 1975).

$$\begin{aligned} Y = FN_0e^{(-Mr)}W_\infty(1/(M+F) \\ - 3e^{(-kr)}/(M+F+k) \\ + 3e^{(-2kr)}/(M+F+2k) \\ - e^{(-3kr)}/(M+F+3k)). \end{aligned} \qquad (3)$$

So, rather than derive analytical expressions (e.g., Sims 1984), I resort below to a simpler approach. Sensitivity of fishery models to changes of given magnitude in M is assessed by comparing percent change reported in model response (output) to percent change in M (input). In cases for vector (age or density-dependent) M, I have merely described the shape of the M-vector. For these different vectors, I report the percent change in the result due to switching from a vector of one shape to a vector of another shape.

Yield Models

At least four studies (Beverton and Holt 1957; Hennemuth 1961; Francis 1974; Bartoo and Coan 1979) have shown that errors in estimates of M propagate into roughly equal errors in estimates of $(Y/R)_{max}$, but with sign reversed (Table 2). For example, a 10% overestimate in M will lead to approximately 10% underestimate of $(Y/R)_{max}$. An equally important result is that the actual magnitude of the effect induced depends strongly not just on the error in M, but on the values chosen for the other parameters in the model.

In another study, Beddington and Cooke (1983) used the Beverton-Hol formulation to investigate the influence of M (constant; 0.1 to 0.8 year^{-1}), t_c (0 to 4 years), and K (the von Bertalanffy growth parameter; 0.1 to 0.5 year^{-1}) on MSY (maximum sustainable yield), expressing the result as "MSY as a % of B_0," where B_0 is the initial or recruited biomass. Higher percentages indicate that more of the original biomass is being taken at MSY. Increasing M by a factor of 8 (0.1 to 0.8 year^{-1}) increased MSY/B_0 by a factor of about 4 to 8, depending on the particular values of t_c and K. Again, errors in M produced roughly the same relative error in the result; and again the actual effect of any given change in M de-

TABLE 2.—Sensitivity of estimated maximum yield per recruit ($(Y/R)_{max}$) to changes in instantaneous rate of natural mortality (M) and other input conditions. Sensitivity of $(Y/R)_{max}$ and of changes in M are expressed as percentage difference from nominal responses at nominal (best-guess) M. Symbols are: t_c = age-at-first-capture, F = instantaneous rate of fishing mortality, M = nominal value for M. Frances (1974) used an age-structured simulation model. All other citations used standard yield-per-recruit analyses.

Input conditions	% change in M	% change in $(Y/R)_{max}$	Species	Source
t_c = constant (3.72) F = variable M = 0.10	+50 −50	−20 +30	plaice	Beverton and Holt 1957
t_c = variable F = constant (0.73) M = 0.10	+50 −50	−60 +50	plaice	Beverton and Holt 1957
F = constant (0.95) M = 0.8	+20 −20	−21 +32	yellowfin tuna	Hennemuth 1961
M = 0.8	+10 −10	−14 +16	yellowfin tuna	Francis 1974
M = 0.60	+25	−20	yellowfin tuna	Bartoo and Coan 1979

pended on the values chosen for the other parameters.

Pope and Garrod (1973) present another example of sensitivity in MSY to values chosen for M. They describe briefly the consequences of using an incorrect constant for M of cod stocks when estimating the F required to generate MSY (F_{MSY}). Underestimating M by 50% (assumed $M = 0.1$ year^{-1}; true $M = 0.2$ year^{-1}) leads to a choice of F_{MSY} that is 67% too high. Overestimating M by 50% (assumed $M = 0.3$ year^{-1}, true $M = 0.2$ year^{-1}) underestimated F_{MSY} by 50%.

The simulations described above tested the effects of choosing alternative constant values for M. Choosing a vector alternative can also have significant effects; again, the magnitude of the effect depends on the values chosen for other parameters. Beverton and Holt (1957) showed that incorporating density-dependence in M for plaice decreased $(Y/R)_{max}$ by 12%, when holding t_c constant at 3.72 years and letting F vary. Conversely, holding F constant and letting t_c vary decreased $(Y/R)_{max}$ by about 37%.

Age-dependent values for M were compared with age-constant values by Bartoo and Coan (1979), Bulgakova and Efimov (1982), and Tyler et al. (1985). In their analysis of Atlantic yellowfin tuna stocks, Bartoo and Coan found that replacing an assumed constant M of 0.8 year^{-1} with an age-structured M increasing from 0.1 year^{-1} at age 0 to 1.2 year^{-1} at age 7, increased $(Y/R)_{max}$ by 17% (from 6 to 7 kg).

Estimating total yield (Y_t) rather than (Y/R) and estimating R as a function of constant versus age-specific M in analysis of catch curves for relatively unexploited stocks of Pacific ocean perch and Oregon hake, Bulgakova and Efimov (1982) found that replacing a constant (age-averaged) M with age-variable M tended to increase estimated Y_t when fish recruited fairly late to the fishery, but decreased Y_t if the fish recruited early. This is because of the interaction between the values assumed for M (constant or age-variable) and the value calculated for R from each type of mortality curve.

Starting with a given value for recruitment at age 6 years (from Efimov 1976), they calculated R twice for ages 4 and 8 years—once with age-averaged M and once with age-specific M. Because in this set of data the age-averaged M was generally higher than the age-specific M at the tested ages of recruitment (ages 4, 6, or 8 years), back-calculations with age-averaged (i.e., constant) M predicted fewer recruits than back-calculations with age-specific M. With fewer recruits and generally higher M, potential yield at later ages obviously must drop. Differences in predicted potential yield ranged from about −30% at t_4 (age-specific estimate lower than age-averaged estimate, when fish were assumed to recruit to the fishery at age 4 years) to +15% at t_6 (age-specific estimate higher) and to +60% at t_8.

Tyler et al. (1985) tested (among other things) the effects of ignoring "true" age-structure in M and using instead a constant value in estimating stock biomass using Deriso's (1980) delay-difference model. They did the tests on catch data generated by Walter's (1969) age-structured simulation model of cod, using three different (input) age structures for M in Walter's model. After generating "catch data" from Walter's model, they analyzed the simulated data set using Deriso's model with constant M (= 0.5 year^{-1}). The age structures tested were 1) mortality increasing and then decreasing with age (Walter's original mortality vector spanning ages 3 to 12 years; age-averaged $M = 0.55$ year^{-1}, range = 0.33 to 0.70 year^{-1}), 2) mortality increasing with age (ages 7 to 12 years; average $M = 0.5$ year^{-1}, range 0.3 to 0.7 year^{-1}) and 3) mortality decreasing with age (ages 7 to 12 years; average $M = 0.5$ year^{-1}, range 0.7 to 0.3 year^{-1}). In all three cases Deriso's model with constant M misestimated the "true" biomass generated by Walter's model (with age-structured values for M). The differences were relatively small, however: −13% for the increasing and then decreasing series, +19% for the decreasing series, and +4% for the increasing series. These differences were due to the differences in M, and not the differences in model structure; generating and analyzing biomass with the same constant M in both models led to a discrepancy of only 0.5%.

By analogy to life history patterns in other adult animals, M (after recruitment into most fished stocks) is more likely to increase with age than to cycle or decrease. By implication, the simulation results from the increasing series are probably most realistic. If so, the effects of ignoring age-structure in favor of using a constant M may be relatively small (5 to 20%), at least for the cod stock simulated in this study. But the results obviously depend again not just on correctly choosing the values for M, but on the values chosen for the other parameters. In this case, Tyler et al.'s (1985) results imply that age-structure in M can be relatively unimportant, at least when the

assumed constant is evenly bracketed by the "true" age-structure in M.

Further simulations by Tyler et al. (1985) using a wide range of constant values for M (0.4 to 1.4 year^{-1}) and the growth rate parameter rho (mean Ford growth coefficient for the fishable stock; 0.46 to 1.6) showed that incorrect guesses of M (and rho) could produce errors up to 1,000% in estimated biomass. More realistic ranges for the two parameters (0.4 to 0.8 year^{-1} for M, 0.6 to 1.2 for rho), extending about 50% above and below the "true" values for these parameters, induced much lower error in biomass estimates (about the same order of magnitude, 50 to 100% below and above the "true" biomass). As before, changes (errors) of a given amount in M (expressed as fraction or percentage of the original value) appear to produce about the same amount of change (expressed as percent of original value) in simple estimates of yield, depending on the conditions of other parameters in the model.

Chatwin (1958) compared estimates of Y_{max} from lingcod populations. Rather than compare constant and age-variable values for M, he assumed several different values for an average (constant) M in adults, but assumed that M increased from the assumed average for adults to higher values in both juveniles and senescent fish. He reports no quantitative results but states, as found above, that increasing the average M, for a given F, considerably decreased Y_{max}, that decreasing M increased Y_{max}, and that size at first capture changed relatively little with those changes in M.

These comparisons between age-structured versus constant M, or between different constants have demonstrated that effects on results can be large for some combinations of parameters yet small for others. Alternative choices drawn from apparently realistic parameter values lead to relatively small differences in estimates of M. Specific amounts of change depend strongly not only on the values chosen for M, but also on the value of M **relative** to values chosen for the other interacting parameters in the yield models. For most choices of parameter values, sensitivity of output is roughly equal to perturbation of input.

Cohort Analyses

Effects of interactions between changes in M and values chosen for other parameters is even more obvious in stock reconstruction analyses (e.g., cohort analysis and virtual population analysis (VPA)). These analyses are used to "reconstruct" estimates of stock abundance during previous years, based on catch data and assumptions about the value(s) of M during those previous years. Studies of sensitivity to M in Beverton-Holt types of yield or biomass assessments were usually empirical, based on analyses of catch data from specific fisheries. Studies of sensitivity to M in VPA and cohort analysis include both theoretical and empirical studies; i.e., simulations using totally contrived data sets (e.g., Agger et al. 1973), analyses of specific data sets (e.g., Pope 1971; Doubleday and Beacham 1982) and combinations of analytical evaluations and analysis of specific data sets (e.g., Doubleday 1976; Ulltang 1977; Sims 1982a, 1982b, 1984).

Simple analyses of sensitivity to M, in which M is varied but all else is held constant, include 1) Pope's (1972) analysis of Atlantic yellowfin tuna, in which he found that replacing constant M with age-structured M (higher Ms for older fish) produced lower estimates for fishing mortality (F_i) in the later ages, but had little effect on estimates for the younger ages, and 2) Doubleday and Beacham's (1982) statement that 10% error in constant M translated into 9 to 14% error in estimates of R (at age 3) for cod in the Gulf of St. Lawrence.

Somewhat more complicated analyses are presented by Ulltang (1977) and Sims (1982a, 1982b, 1984). Ulltang evaluated the effects on model predictions of F_i and N_i, of several types of variation in M. These included no variation (uniformly constant M), M constant within years but varying randomly between years, M varying with age, and M varying with season. Sims evaluated the effects of choosing various constants for M on estimates of N_i, and derived an analytical expression relating variance in M to expected variance in estimates of abundance.

In Ulltang's simulations, increasing (decreasing) a constant M by 50% (from 0.2) decreased (increased) F by about 20% ("true" F's ranging from 0.4 to 0.8). Creating a data set with M varying randomly from one year to the next, then analyzing those data with an assumed constant M, Ulltang (1977) found that the Z calculated from the constant-M model was on average the same as the "true" Z from the random-M model. He concluded that random fluctuations in M will cancel out during analysis and so can be ignored. Ulltang assessed the influence of age-dependent M compared with constant M by generating a catch curve with age-variable M (decreasing curvilin-

early from 0.3 at age 1 to 0.1 at age 10, average about 0.2) and F equal to 0.2, then analyzing the catch with F equal to 0.2 or 0.6, and M equal either to 0.1 or 0.2. Choice of M made little difference in estimates of stock size for the case of high F (0.6), because most of the deaths were due to (observed) fishing. When F was low (0.2), stock-size estimates were much more sensitive to incorrect choices for M, because most of the deaths were due in this case to M, which was unmeasured and therefore unobserved.

Ulltang (1977) simulated seasonal changes in M by concentrating all deaths in either the first or last quarter of a year. Estimated stock sizes (N_i) changed relatively little; with $F = 1.2$ and $M = 0.4$, N_i was a maximum of 10% higher if all deaths occurred first quarter, 10% lower if all occurred in the last quarter.

A serious problem with the conclusions reached by Ulltang (1977) is also common to all the other studies discussed above; they are based on relatively few combinations of values for the various parameters, and relatively few simulations. For example, the conclusion that random errors in M will tend to even out is intuitively attractive, provided the time scale of variation is short relative to the generation time of the fish. In fact random variation in M did even out in the two sets of simulations he conducted. But the examples he chose included only one set of ages (2 to 10 years), with relatively high values of F (0.5 to 0.8 year^{-1}) compared to the values tested for M (0.1, 0.3 year^{-1}). The gravity of consequences from choosing an incorrect M depends very heavily on the size of M **relative to** the size of F, i.e., on E. Had he chosen different values for his simulations, he might have reached very different conclusions. This is probably the basis for the discrepancy between Ulltang's conclusion that seasonal effects are minor, versus Sims' (1984) conclusion that seasonal effects can be quite large, if M is high.

Sims (1984) attempted to overcome this problem (trying to draw general conclusions from the results of simulations based on particular, or relatively few, sets of parameters) by analytically deriving formulas for relative error in stock-size estimates, and then testing the formulas with data from actual fisheries. He used this approach twice: once to assess the effects of seasonality (Sims 1982a) and once to consider in general the effects of different choices (errors) for constant M (Sims 1984). But his results (and equations for error) show clearly that error in estimated stock sizes depends on several parameters and that the effects of one can be strongly dependent on the values chosen for the others. Choosing a high M (0.6 year^{-1}) and concentrating catch during the first quarter of the year overestimated R by 20%; concentrating catch during the last quarter underestimated R by 23% (compared with the 10% error found by Ulltang).

Within the same analysis, reducing M by half (to 0.3 year^{-1}) reduced the error in R by half, but the same reduction of error in R was also achieved by leaving M high and reducing F. In assessing specifically the effects of error in M on error in R, Sims (1984) showed very different effects on estimates of R in heavily fished versus lightly fished cohorts of Atlantic bluefin tuna. Changing M by 50% led to changes in estimated R of 60 to 260% in the lightly fished cohort, but only to relatively smaller changes of 35 to 70% in the heavily fished cohort. Again, the magnitude of the error in model predictions depended not just on the magnitude of M, but on its relationship to the other parameters in the catch equation, particularly F.

Errors (expressed as percentage change in output for a given change in input) in model output in the simulations described above, all of which tried to use apparently realistic values for model parameters, rarely exceeded 50%, and were often less than the error introduced into values chosen for M. By implication, the effects of incorrectly guessing M may be relatively unimportant if M is relatively small (e.g., in this situation not more than about 0.5 year^{-1}) and relatively invariant, although the actual magnitude of effect due to any given percentage change in M depends on the values chosen for other parameters.

So, inaccurate estimates of M might be important or they might not. It all depends on the magnitude and variability of M within a **given stock** (or group). Although untested, it seems likely that estimates of M for groups in which M varies little and is relatively low, are more likely to be reasonably accurate than estimates of M from groups in which M is large and variable. The following section reviews evidence that M does in fact vary both within and between groups of fish, and the succeeding section reviews evidence for the magnitude of that variability in ostensibly similar groups.

IV. FACTORS INFLUENCING DEATH RATE

Despite the fact that in most fishery models, M is assumed to be constant for all exploited ages in

any given stock, abundant evidence exists to the contrary. Natural mortality has been shown to vary with age, density, disease, parasites, food supply, predator abundance, water temperature, fishing pressure, sex, and size. Evidence for relationships between these factors and M, and selected references for each, are presented below.

Changes in mortality rate with **age**, within single groups of fish, have been demonstrated and discussed more frequently than changes with any other factor. References include, among others, Baranov (1918, plaice), Sette (1943, Atlantic mackerel), Ricker (1945, 1947, lake fish; 1969, 1975, various species), Beverton and Holt (1959, many species of marine fish), Beverton (1963, engraulids and clupeids), Boiko (1964, sturgeon), Cushing (1975, plaice), Blinov (1977, fish in general), Bulgakova and Efimov (1982, Oregon hake and sea perch), Sandland (1982, fish in general), Smith (1985, clupeoids), Roff (1986, fish in general). Evidence for changes with senescence for fish in general has been discussed or documented by, among others, Woodhead (1979) and Craig (1984).

Although specific patterns vary with species (e.g., Woodhead 1979), in general M is extremely high during egg and larval stages (e.g., 2 to 10% per day in plaice and clupeoids (Cushing 1975; Smith 1985)), falls precipitously during the juvenile period, becomes **relatively** stable during intermediate adult ages and increases again with senescence. But even during these relatively stable mid-adult ages, changes in M with age can be substantial, particularly in short-lived fish (e.g., Ricker 1947, stunted versus "normal" whitefish).

Changes in natural mortality rate with **size** (rather than age) within single groups of fish (usually stocks), have been discussed by Baranov (1918, plaice), Ricker (1969, size-selective mortality in general), Ware (1975, larval fish), and Peterson and Wroblewski (1984, many species). Differences in natural mortality rate between populations of the same species in different environments, or even in different areas of a single environment (e.g., a single lake) are documented by Ricker (1947), Kennedy (1954), and Schupp (1978). Year-to-year differences in natural mortality rates of single stocks from a given area are shown by Pope and Knights (1982, plaice) and by Henderson et al. (1983, whitefish). Density-dependent changes in M are discussed by Beverton and Holt (1957), Cushing (1967), Tyler and Gallucci (1980), Backiel and LeCren (1978), Jones (1982), and others. Differences in M between sexes have been documented by Beverton and Holt (1957, plaice), Ricker (1947, rock bass), and others. Changes in natural mortality rate related to the cost of reproduction have been discussed by Jones and Johnston (1977), Roff (1984), and others.

Other factors that affect M either alone or in combination with other factors include disease and parasitism (reviewed by Lester 1984), starvation (Hewitt et al. 1985; Theilacker 1986: larval anchovy), physiological state (Smith 1985), and fishing pressure (Ursin 1982; Munro 1982). Additional examples are cited by Beverton and Holt (1957), Anderson and Ursin (1977), Sissenwine (1984), and Hunter (1984).

Most of the factors listed above (e.g., age, size, sex) are indirect influences on M. The most important factor directly affecting natural mortality rate is probably predation; this is implied by a large body of literature describing changes in prey community composition and abundance following changes in composition and abundance of predators (e.g., Carpenter et al. 1985).

Direct evidence that predators account for most natural mortality in fish stocks is difficult to gather (Section II). To quantify the fraction of M due to predation, one must know, not only relative changes in abundance, but absolute population density of all predators and prey together with consumption rates and prey preferences of all the predators. Although this is rarely possible, at least two studies from freshwater systems do present quantified estimates of predatory mortality in relation to available prey. Forney (1977) quantified predation mortality in a relatively simple, unmanipulated lake system where there were few species of predator and prey. Combining stomach-content estimates of prey consumed with trawl-sample estimates of predator and prey abundance, he concluded that 30 to 100% of yellow perch production was consumed by walleye, their principal predator. In a manipulated system, Stein et al. (1981) assessed predatory mortality of young tiger muskellunge after they were stocked in a small pond and lake. During the time of the study, a single predator (largemouth bass) accounted for 25 to 45% of losses to natural mortality.

In marine systems evidence for the relative importance of predation can be gleaned from comparing total natural mortality with estimated predatory mortality based on abundance of predators and feeding preferences. For example, multispecies cohort analyses reported by Pope and

Knights (1982) show predatory mortality as 80 to 90% of M for age-0 cod, whiting, and haddock in the North Sea (the fraction of M due to predatory mortality cannot be assessed accurately in the older ages because predators appropriate to these sizes were not included in the analysis). In another example, estimating M from energy flow models, Sissenwine (1984) demonstrated that predation in the Georges Bank ecosystem can account for all production by prey fish; nonpredatory mortality was negligible.

Thus a multitude of factors, acting alone or in concert, can be expected to produce variations in M between individuals within single groups of fish, as well as between groups. Differences can be expected between species, between stocks within species, and from place-to-place and time-to-time within given stocks. In the following section, I will review more completely existing evidence for, and the extent of, this expected variability in M.

V. VARIABILITY WITHIN AND BETWEEN GROUPS

As discussed above (Section III), simulation studies generally show that effects of choosing a particular value or set of values for M can range from insignificant to considerable, depending in part on the model used, in part on the values chosen for other parameters, and in part on the form chosen for the estimate(s) of M. Authors suggest that in the future, simulations should be conducted with a range of values for M, to bracket probable values (e.g., Beverton and Holt 1957; Tyler et al. 1985).

The problem with this advice is identifying the appropriate range and distribution of M for any given group of fish. Obviously, wide ranges for M will lead to great discrepancies between model predictions based on one end of the range or the other. It has been shown above, however, that model output can be relatively **insensitive** to small changes in M. This is particularly true if F is much larger than M (i.e., if the stock is highly exploited so that losses to fishing far exceed losses to natural mortality). The problem is determining whether, for a given stock in situ, changes in M are in fact large or small. Compensatory changes in M, in response to changes in F, will further confound the problem, because variations in M will then be a function of the value(s) of F, in addition to the suite of other factors that may be affecting estimates of M.

M does appear to vary considerably **between** groups of fish. Estimates of M compiled by Pauly (1980) (Fig. 1) for 175 stocks and species of fish worldwide differ greatly between groups, ranging from a minimum of about 0.1 year^{-1} to several unusual values as high as 7.0 year^{-1}. Even within a group as ostensibly homogeneous as the tunas, the range of estimated mortality constants spans the majority of the common values (0.2 to 2.0 year^{-1}, Murphy and Sakagawa 1977).

Estimates of variability in M **within** groups of fish are much less common, but are actually more important than the obvious differences between groups with obviously different characteristics such as differing lifespans. Most fishery analyses are directed toward understanding or predicting dynamics of single stocks (single groups of fish). The most important considerations for natural mortality parameter values in these single-species analyses are whether and if so over what values M varies for the group of fish in question.

But measuring trends or variability in natural mortality rates **within** given groups (e.g., stocks) is difficult and, with the exception of trends with age, rarely attempted. This is primarily because the only extant methods for estimating M depend either directly or indirectly on analysis of catch data (Section II), and catch data are prone to many well known (but largely unsolved) problems.

Problems with analysis of catch data fall into two general categories: 1) problems with sampling procedure, such that fish are caught or counted out of proportion to their true abundance and 2) problems with fish appearing or disappearing from the "unit stock" due to causes other than birth or natural mortality (i.e., migration, fishing mortality, or tagging mortality), again resulting in catch data that do not represent the true structure of the stock. If sampling biases can be overcome, the problem reduces to partitioning total disappearance of fish into fractions owing to fishing, tag mortality, and migration. The first partition can be eliminated by studying unfished populations, the second by quantifying tag mortality, and the third by studying only closed or tagged populations.

Unfortunately, very few sampled populations satisfy completely even one of these criteria. Regardless, we still need at least some crude estimates of M in order to determine whether M truly varies enough to invalidate the standard assumption in fisheries models that M is effectively constant during exploited ages. The question here

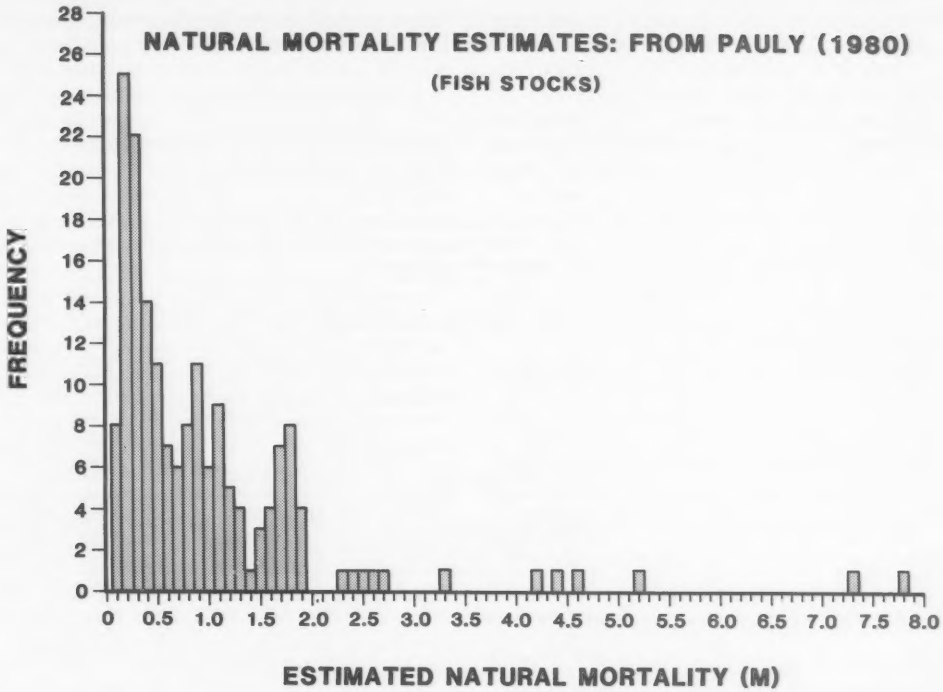

FIGURE 1.—Frequency of estimated instantaneous annual rates of natural mortality (M) in 175 different fish stocks, populations, or species. Estimates include both freshwater and marine species. Data from Pauly 1980.

concerns variability of M **within** groupings that would be used commonly to estimate M, such as stocks of single species, rather than general patterns across species. If M truly varies relatively little during these ages (so that the log of catch-at-age decreases linearly with age), if the age structure has been relatively constant historically (so that catch curves are actually linear, rather than curvilinear as seen in stocks with inconstant age structure, e.g., chapter 2, Ricker 1975), and if catch curves actually reflect relatively accurately this constancy and low variability, then most estimates of M derived from analysis of appropriately processed catch curves cannot help but be relatively close to the true rate. Model predictions, although in theory sensitive, would in practice be fairly robust to any particular value chosen from the true range of values for M.

Despite the potential problems with accuracy or precision of existing estimates from single groups of fish, I list in Table 3 most of the estimates available for unexploited populations, and some of the few existing estimates from exploited populations. My purpose is to identify the apparent range of variability in M within single stocks. The estimates are drawn from references cited by Pauly (1980) and other sources. Only references that reported multiple estimates for M are included, thus excluding most of the references reviewed. Because these estimates are derived from catch data, the stated ranges are "apparent", rather than demonstrably the "true" values.

Estimated rates of natural mortality are not particularly constant for either unexploited or exploited groups, and are only slightly less variable within stocks than they are within species. Although the range of rates within groups may appear relatively small compared to the total range of rates reported for all fish species (e.g., 0.36 to 0.56 for sauger from Lake Nipigon [Table 3] vs. approximately 0.1 to 3.0 for most species listed by Pauly 1980), the maximum and minimum rates reported for single groups differed by at least 50% in 20 of the 22 comparison listed in

Table 3. In at least one case maximum and minimum estimates differ by as much as a factor of 7 (i.e., young vs. old whitefish in Shakespeare Island Lake, Ricker 1947, Table 3).

The range of reported estimates of M for species (rather than single groups or stocks within a species as compared above) is even greater. Even the least variable estimates differed by a factor of 1.75 (75%, male vs. female plaice, Beverton 1964). In whitefish, the species for which the most estimates exist, maximum estimates are **20 times** greater than minimum estimates (Table 3).

TABLE 3.—Ranges in estimates of instantaneous rate of natural mortality in unexploited and exploited fish populations. M_{max}/M_{min} is expressed as the ratio between the maximum (M_{max}) and minimum (M_{min}) values reported for M for that species, Values in parentheses are total range of estimates and ratios for those species where multiple reports exist.

Species name	Common name	Body of water	Sex	Age (years)	M range	M_{max}/M_{min}	Source
I) Unexploited populations:							
Amboplites rupestris	rock bass	Nebish Lake	m	10–12	1.47–2.1	1.49	Ricker 1947
		Nebish Lake	f	10–14	1.1–1.6	1.45	Ricker 1947
		Nebish Lake	both	10–14	1.08–1.56	1.44	Ricker 1947
					(1.08–2.1)	(2.01)	
Stizostedion canadensis	sauger	Lake Nipigon		8–14	0.36–0.56	1.56	Ricker 1947
Coregonus clupeaformis	whitefish	Lake Opeongo		6–13	0.53		Ricker 1947
		Shakespeare Island Lake		11–27	0.08–0.60	7.51	Ricker 1947
		Great Slave Lake		17–22	0.71–0.99	1.39	Kennedy 1953
		Lake Nueltin		13–15	0.84		Kennedy 1963
		Lake McDonald		11–14	1.34		Kennedy 1963
				9–10	1.66		Kennedy 1963
					(0.08–1.66)	(20.75)	
Leucichthys sardinella		Ikroavik Lake		6–10	0.2–1.4	7.00	Wohlschlag 1954
Cristovomer namayacush		Great Slave Lake		1–26	0.31–1.61	5.19	[1]Kennedy 1954
		Great Slave Lake		15–23	0.49–0.92	1.88	[1]Kennedy 1954
		Great Slave Lake		15–23	0.52–0.75	1.44	[2]Kennedy 1954
					(0.31–1.61)	(5.19)	
Perca fluviatilus	perch	River Thames	m	3–8	0.56–0.98	1.75	Williams 1967
		River Thames	f	3–7	0.2–0.64	3.20	[3]Williams 1967
		River Thames	juv	3–5	0.53–1.69	3.19	[3]Williams 1967
					(0.2–1.69)	(8.45)	
Leuciscus leuciscus	dace	River Thames		5–11	0.36–1.31	3.64	[4]Williams 1967
Alburnus alburnus	bleak	River Thames		3–8	0.6–2.4	4.00	[4]Williams 1967
Rutilus rutilus	roach	River Thames		2–11	0.22–1.38	6.27	[4]Williams 1967
		River Stour		3–12	0.44		Mann 1973
					(0.22–1.38)	(6.27)	
Cheilodactylus macropterus	tarakihi	Chatham Islands		5–35	0.03		Vooren 1977
		Chatham Islands		5–22	0.08		Vooren 1977
		New Zealand			0.15		Vooren 1977
					(0.03–0.15)	(5.00)	
II) Exploited Populations:							
Pleuronectes platessa	plaice	North Sea	f	5–13	0.08		Beverton 1964
		North Sea	m	5–13	0.14		Beverton 1964
					(0.08–0.14)	(1.75)	
Brevoortia petronus	gulf menhaden	Gulf of Mexico, Central (1969, 1971)		1–3	0.7–1.6	2.29	[5]Ahrenholz 1981
		Gulf of Mexico, Eastern (1969, 1971)		1–3	0.88–0.98	1.11	[5]Ahrenholz 1981
		Gulf of Mexico, Western (1969, 1971)		1–3	1.17–1.23	1.05	[5]Ahrenholz 1981
		Gulf of Mexico, all areas (1969, 1971)		1–3	0.95–1.2	1.26	[6]Ahrenholz 1981
					(0.7–1.6)	(2.29)	
Gadus morhua	cod	North Sea		0.5–1	0.59–1.46	2.47	[7]Pope and Knights 1982
Coregonus clupeaformis	whitefish	Lake Huron		3.8	0.34–1.67	4.91	[8]Henderson et al. 1983

[1]Increasing with age.
[2]Year to year variation (1946–52); ages 15–23 combined.
[3]Not consistent with age.
[4]Generally increasing with age.
[5]Assuming 20% tag loss rate.
[6]For tag loss rates from 10 to 30%.
[7]8 different years (1967–75).
[8]23 different year classes (1947–75).

As discussed previously, these different estimates can lead to at least as great a difference in results produced by fishery analyses such as yield models or stock reconstruction analyses (Section II).

Reported differences in estimates of M for whitefish stocks living in Shakespeare Lake compared with other relatively small lakes (e.g., Lake McDonald, Table 3) are particularly significant. Because both stocks are of the same species and living in more or less similar environments (small lakes), one might easily (and incorrectly) assume that both have the same rate of natural mortality; but they did not. The lower rates occurred in the stock occupying a small lake with no predators. This is a clear example of the effect that environment, particularly the predator environment, can have on the realized rate of natural mortality in a fish stock. Obviously, choosing a single appropriate constant for this species would be difficult. Choosing an appropriate species-specific constant for some of the other species with multiple estimates might be difficult as well (e.g., rock bass, lake trout, perch, roach, tarakihi, or menhaden, Table 3).

None of these studies from either unexploited or exploited stocks support the assumption that M is constant for any given stock or species, nor are these within-stock ranges particularly narrow. In addition, treatment of the original catch data may have in some cases obscured the "true" variability. Ricker (1947) and Kennedy (1953, 1954, 1963), for example, use a 3-yr smoothing technique to reduce the effects of unequal recruitment; this also serves to reduce variability that may actually be due to differences in natural mortality. Also, single estimates from data collected during only one or two years of sampling (e.g., Wohlschlag 1954; Williams 1967; Mann 1973; Vooren 1977) can be seriously biased by annual changes in either recruitment or mortality rates. If the estimates reported above are even approximately accurate, it is apparent that the range of possible values for M is wide, and that variability can be considerable even within single stocks.

A solution to this problem of choosing a reasonable value for M, at least for long-lived fish, is suggested by the possibility that **variation** in M (not just the mean value) may be related to maximum lifespan. Fish that live for many years must naturally have lower mortality rates than more short-lived fish. These lower rates may also be less variable in the longer lived stocks, if as in many other biological processes, variability is proportional to the mean. This could account for the ubiquity and apparent effectiveness of the constant 0.2 year^{-1}, used almost universally for the long-lived (20 to 30 years) and well-studied fish stocks from northern European seas (e.g., Beverton 1964). If so, assuming a constant M might be valid for these longer lived stocks.

Unfortunately, the few studies cited above do not support this attractive idea. Although in general, mortality rates decease as lifespan increases, the variability in estimates does not appear to follow the same trend. This may be due partially to the relatively similar lifespans (10 to 20 years) for most of the species for which estimates exist. But the apparent range in rates for the shortest lived species cited above (Ahrenholz 1981, *Brevoortia patronus*, ages 1 to 3 years, M range 0.7 to 1.6 year^{-1}) is certainly not greater than ranges reported for the longer lived whitefish (Henderson et al. 1983, *Coregonus clupeaformis*, ages 10+ years, M range 0.34 to 1.67 year^{-1}).

VI. SUMMARY AND RECOMMENDATIONS

Thus it appears that rates of M, or at least rates of M derived by existing estimation methods, do in fact vary widely within many fish stocks. Because the variations appear to be considerable and because the results from fishery models can be sensitive to large variations in M, one must conclude that assuming constancy without proof can have serious consequences for fishery management.

A better approach may be to discard the notion that a single "best" estimate of M can be found, and instead try to tailor estimates of M to local groups, based on some combinations of the methods discussed in Section III. Obviously, practical considerations of time and resources will limit the accuracy and precision with which M can be estimated. Also, the estimates in the studies reviewed here are prone to all the artifacts mentioned in the previous sections. True rates of natural mortality, and their variability, are still very poorly known for even the great stocks of commercial fish in temperature regions that have been subject to continuous exploitation for decades. Careful, repeated tagging experiments probably hold the most promise for determining with any reasonable degree of accuracy, rates of natural mortality in fish stocks. But even these have inherent problems that are not easily

solved. There remains a great need both for new methods, and refinements of the old.

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NATURAL HISTORY OF THE RAYS OF THE GENUS *MOBULA* IN THE GULF OF CALIFORNIA

GIUSEPPE NOTARBARTOLO-DI-SCIARA[1]

ABSTRACT

Mobulid rays, which abound during summer in the southern Gulf of California, southern Baja California, Mexico, were monitored for a period of four years during a study of their biology. A total of 262 specimens belonging to four species of *Mobula* were examined. *Mobula thurstoni* was the most abundant (58% of the catch), followed by *M. japanica* (30%), *M. munkiana* (9%), and *M. tarapacana* (3%). The study area served as a nursery ground for *M. thurstoni*, a summer feeding and mating ground for *M. thurstoni* and *M. japanica*, and a wintering ground for *M. munkiana* and young *M. thurstoni*; *M. tarapacana* was rare. Data on size, weight, sex ratio, life history, seasonality, feeding habits, behavior, habitat, and symbionts are presented for each species. Size segregation was a common feature of *M. thurstoni*, *M. japanica*, and *M. munkiana*; sex segregation was not evident. An extreme degree of feeding specialization was noted: summer prey were almost exclusively the euphausiid *Nyctiphanes simplex*; the mysid *Mysidium* sp. dominated in the winter. A key to the genus *Mobula* in the Gulf of California is presented as an aid for species identification.

This paper reports on natural history aspects of rays of the genus *Mobula* (Mobulidae), a poorly known group of elasmobranchs commonly called manta rays or devil rays, frequent in the Gulf of California. A good early overview of the family Mobulidae was given by Gill (1908). Cadenat (1960) described the natural history of the mobulids of tropical west African waters, based on specimens which were occasionally captured by the local fishermen. However, with the exception of observations carried out with some regularity by Coles (1910, 1913, 1915, 1916a, 1916b) of *Mobula olfersi* (= *M. hypostoma*) and *Manta birostris* off North Carolina, most of the available literature is purely anecdotal and deals with occasionally encountered or harpooned specimens. Long-term field investigations of devil ray ecology and behavior are wanting. As a result, mobulids are among the least known of the batoid taxa. This was recognized by Bigelow and Schroeder (1953) in their comprehensive review of the knowledge of this family. No major contribution to the understanding of any aspect of mobulid biology has since been published.

Regular fisheries for mobulids were not known to exist, because mobulid meat is generally considered of little market value. However, in 1981, during a reconnaissance trip to the southern Gulf of California (Mexico), in the vicinity of La Paz, Baja California Sur, a regular, seasonally important fishery was discovered. This activity afforded the opportunity to study several aspects of the natural history and the ecology of these batoids.

Preliminary oral interviews revealed that local fishermen in the Gulf of California knew of, and routinely captured, four species of devil rays, in addition to the well-known giant manta ray, *Manta birostris*. This information contrasted with the scientific literature, where only two mobulid species, *Manta birostris* and *Mobula lucasana*, were reported for the area (Beebe and Tee-Van 1941; Fowler 1944; Castro-Aguirre 1965). The confusing state of mobulid taxonomy demanded a revisionary work of the genus *Mobula* (Notarbartolo-di-Sciara 1987), and a discussion of the systematics of *Manta* in the eastern Pacific (Notarbartolo-di-Sciara in press). Such effort permitted designation of names for all species of *Mobula* found in the Gulf of California: *M. thurstoni* (Lloyd 1908), of which *M. lucasana* Beebe and Tee Van (1938) is a junior synonym; *M. japanica* (Müller and Henle 1841); *M. tarapacana* (Philippi 1892); and *M. munkiana* Notarbartolo-di-Sciara (1987), which had not been described before. Many of the reports of *M. lucasana* (= *M. thurstoni*) from Central and South America (Beebe and Tee-Van 1941; Fowler 1944; Nichols and Murphy 1944; Barton 1948; Castro-Aguirre 1965; Chirichigno 1974; Pequeño 1983) undoubtedly refer to other species of *Mobula*. A key to the genus *Mobula* in the Gulf of

[1]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093; present address: Museo Civico di Storia Naturale, corso Venezia 55, 20121 Milano, Italy.

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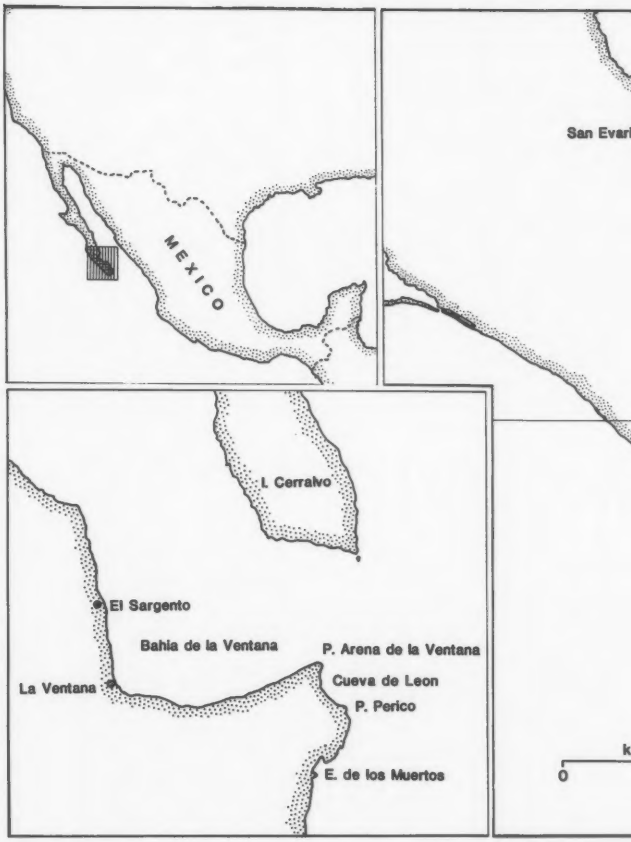

FIGURE 1.—The study ar

110° W
n Evaristo
L El Pardito
LA PAZ
24° N
Los Frailes
San Jose del Cabo
km
50

udy area.

California is presented as an aid to future studies of mobulids from this region.

Working relationships were established with the local fishing communities, and their activities were intermittently monitored between 1981 and 1984. Captured rays were examined and measured before their pectoral fins were filleted; stomach contents and reproductive organs were examined later. Information was gathered on size, weight, sex ratios, life history, seasonality, feeding habits, habitat, behavior, and symbionts of four species of rays belonging to the genus *Mobula* (*M. thurstoni*, *M. japanica*, *M. munkiana*, and *M. tarapacana*). Detailed descriptions and morphometrics of those species are given by Notarbartolo-di-Sciara (1987). The manta ray, *Manta birostris*, was also occasionally captured (Notarbartolo-di-Sciara in press), but is not treated in the present study.

METHODS

Although mobulids are locally said to be abundant on both sides of the southern Gulf of California, for logistic convenience collecting trips were made only to the peninsular coast (Fig. 1). The fishing cooperative based at Punta Arena de la Ventana was selected as the prime collecting site, because mobulids were caught there more consistently than at other localities. Fishing camps on Isla El Pardito, at Cueva de Leon, Ensenada de los Muertos, and Bahia de los Frailes were also sources of study material. Other fishing communities, such as Juncalito, San Evaristo, El Sargento, La Ventana, and San Jose del Cabo were occasionally visited, but yielded no data because mobulids were not specifically sought by the fishermen. Seven field trips were made. Six were short-term (24 January–8 February 1981, 25 November 1981, 16–21 December 1981, 20–23 December 1982, 19–26 January 1984, and 28 October–1 November 1984); one lasted almost six months (26 January–15 July 1983).

Mobulids of all available species and sizes are caught with nets and harpoon; their meat is filleted out of the pectoral fins for human consumption and used as shark bait. Gill nets are either strung just under the surface or are set on the bottom perpendicular to shore, usually at depths between 10 and 200 m. Fishing vessels were 5–7 m fiberglass launches, locally called "pangas", powered by an outboard engine. Fishing occurred within a radius of about 15 km from a base camp. Nets are checked once a day, early in the morning. Rays weighing up to approximately 100 kg were hauled on board, larger specimens were towed ashore. Rays that were dead in the nets, after several hours (i.e., three unsexed specimens of *Mobula thurstoni*), were often partially destroyed by gammarid amphipods (locally called "plaga"), and were unmarketable.

Specimens were weighed and measured before being processed by the fishermen. Weights (WT) were taken with calibrated spring-scales. Rays lighter than 20 kg were weighed to the nearest pound with a 50-lb scale; weights were subsequently converted to kg. Heavier rays were weighed to the nearest kg with a 150 kg scale. Specimens which exceeded 150 kg (all postnatal *M. tarapacana*) were cut in four pieces and weighed separately. Ten percent was then added to the total weight to compensate for body fluid loss. All the specimens could not be weighed, as occasionally a large number of rays were beached simultaneously, and because of the intense heat the fishermen could not delay their processing.

A set of 29 measurements was taken for morphometric analysis and systematic purposes. Methods and results are presented in Notarbartolo-di-Sciara (1987). Measurements relevant to the present paper were disc width (DW), greatest dimension between outermost tips of pectoral fins, pelvic fin length, from anterior margin of vent to tip of pelvic, and clasper length, from anterior margin of vent to tip of clasper. Most specimens were discarded after measuring and sampling. All preserved specimens were deposited in the Marine Vertebrate Collection of the Scripps Institution of Oceanography. Raw data listing all specimens examined and preserved can be found in Notarbartolo-di-Sciara (1985).

The size and shape of the testes were inspected in male specimens, and the ducti deferentes were cut slightly above the genital papilla. Presence or absence of seminal fluid was determined by running a finger in the caudal direction over the ducts anterior to the cut. Clasper length in thousandths of disc width (DW) was plotted against DW to determine size at maturity, and the presence or absence of seminal fluid was noted. Relative size and contents of uteri and nidamental glands were examined in female specimens, and right and left ovaries were compared. The diameter of the largest ovum was plotted against DW to determine size at maturity of female *Mobula*. Eggs were extracted from the germinative epithelium and their greatest di-

ameter was measured to the nearest 0.1 mm with a steel dial caliper.

Stomach contents, if not larger than approximately 200 cc, were sampled whole; otherwise, the bolus was made homogeneous by stirring, and about 200 cc were preserved. Stomach content samples were fixed and preserved in 10% buffered formalin. The stomach content of each sample was thoroughly agitated, separated with a plankton strainer (mesh size 0.5 mm), rinsed of formalin in deionized water, and blotted for 30 seconds on blotting paper. The lump was then molded into a cylindrical shape, and a portion of one end was separated to make up 1 g of wet weight, measured to the nearest 0.1 g. The subsample was then placed with water in a gridded tray, and examined under a dissecting microscope. Contents of the spiral intestine were discarded, because the small crustacean prey was rapidly digested.

Feeding habits were analyzed quantitatively by computing the Index of Relative Importance (%IRI) (Pinkas et al. 1971; Hyslop 1980) for each prey species. The IRI combines percentage by number (N), mass (M), and frequency of occurrence (F) in the formula:

$$\text{IRI} = (\%N + \%M) \times \%F$$

Prey items were identified, when possible, to lowest taxa or species, then the $\%N$ of all prey species within each subsample was calculated. When more than one species was present, all items were individually counted. To obtain the $\%M$ term of the equation, mean mass was calculated for each species by measuring the length of each item contained in five randomly selected squares on a tray, calculating the average length of each prey species, and obtaining mass values from Miller's (1966) Plankton Conversion Tables, where mass is related to length for all main planktonic taxa. The $\%N$ from all subsamples were summed, and the percent from the new sum was calculated, to calculate %IRI for each prey species. The same procedure was applied to $\%M$ and $\%F$. The total $\%N$ was then added to the total $\%M$, and that sum was multiplied by the total $\%F$, to obtain total IRI for each prey species, from which the %IRI was calculated. When few items (e.g., copepods) were found among a large amount of partially digested euphausiid or mysid shrimps, the possibility of reconstructing the shrimp number within the subsample by counting the digestion-resistant eye pairs was discarded to avoid bias in favor of the shrimp fraction. The following method was adopted instead: all odd prey items were counted and measured, and their total mass was obtained from Miller's tables; this was subtracted from the total weight (1 g) of the subsample. The remaining weight was divided by the mean weight of each individual item, calculated by averaging the lengths of all available intact specimens, and obtaining the corresponding weight in Miller's tables. A potential biasing factor existed, when only a few prey remains were found (e.g., when a relatively uncommon item occurred alone in a stomach, therefore contributing a value of 100 $\%N$ and $\%M$ to the total IRI). This factor was avoided by considering, for quantitative treatment, only those stomachs which contained more than 1 g (wet weight) of recognizable food. All stomachs that had <1 g of contents were in fact virtually empty, and the few items found in them were treated only qualitatively.

Remoras were fixed in 10% formalin, preserved in 50% isopropanol, and deposited in the Marine Vertebrate Collection, Scripps Institution of Oceanography. Parasitic copepods were fixed and preserved in 50% isopropanol and sent to the Long Beach State University for taxonomic identification and study.

RESULTS AND DISCUSSION

A total of 262 mobulid rays, belonging to four species (*Mobula thurstoni*, *M. japanica*, *M. munkiana*, and *M. tarapacana*) were examined between 1981 and 1984. Of these, *M. thurstoni* was the most abundant species, constituting 58% of the total catch, followed by *M. japanica* (30%), *M. munkiana* (9%), and *M. tarapacana* (3%).

KEY TO THE SPECIES OF *MOBULA* IN THE GULF OF CALIFORNIA

Mobula can be distinguished from *Manta* by the mouth on the lower surface of the head rather than being subterminal, and by the presence of toothbands in both jaws. Moreover, *Manta* grows to a greater size, and the size of its head, relative to the body, is much greater than in *Mobula*.

1a. Branchial filter plates fused .... *M. tarapacana*
(Spiracle in an elongated longitudinal slit, dorsal to plane of pectoral fins. Teeth tessellated, surface of crown pitted, buccal edge comblike. Thick cover of acumi-

nate denticles. Large adult size, often exceeding 3 m in width. Dorsal side greenish brown. Ventral side anteriorly white, posteriorly gray).

1b. Branchial filter plates separate 2

2a. Spine on base of tail ..... *M. japanica* (Tail very long with a line of white tubercles on both sides. Spiracle a short transversal slit, dorsal to plane of pectoral fins. Teeth not in contact with each other, at least twice as high as the crown is wide; crown subtriangular in apical view. Medium-large adult size, approaching 2.5 m in width. Dark blue to black on dorsal side, apex of dorsal fin white; ventral side white. Skin rough to the touch).

2b. No spine on base of tail ..... 3 (Spiracle small, subcircular, ventral to plane of pectoral fins. Skin smooth to the touch).

3a. Base of tail dorsally depressed .... *M. thurstoni* (Double curvature of anterior margin of pectoral fin. Surface of tooth crown rugose. Medium adult size, exceeding 1.8 m of width. Dark blue to black on dorsal side, apex of dorsal fin white; ventral side white, with a dark greenish patch near the posterior margin of each pectoral fin, and with a pattern of dark and shiny silvery pigmentation on distal half of pectorals).

3b. Base of tail laterally compressed .... *M. munkiana* (Anterior margin of pectoral fin straight to weakly convex. Surface of tooth crown smooth. Small adult size, barely exceeding 1 m of width. Dorsum mauve gray; ventral side white, tips of pectoral fins gray).

Mobula thurstoni (Lloyd 1908) Local name: cubana de lomo azul

Eighty one males (disc width range 630–1,770 mm), 69 females (210–1,801 mm), and three specimens of undetermined sex (941–1,494 mm), were caught at four stations (Punta Arena de la Ventana, Cueva de Leon, Ensenada de los Muertos, and Isla El Pardito) and their adjacent waters, between 7 February 1981 and 30 October 1984. Overall and seasonal size-frequency distributions for *M. thurstoni* are given in Figure 2. Mean size varied with season, smaller rays being dominant in winter catches, medium sizes prevailing in the summer. The difference between mean disc width (DW) in winter and overall mean DW is highly significant (T-value = 5.189, df = 169, $P << 0.001$). There were no significant differences between male and female DWs (T-value = 0.3767, df = 145, $P > 0.5$), with the exception of the November to February period, when females were larger (T-value = 2.331, df = 12, $P < 0.05$).

A total of 105 specimens (210–1,770 mm DW) were weighed. The WT/DW relationship is best described by the equation:

$$WT = 4.817 \times 10^{-8} (DW)^{2.78}$$

$$r = 0.99$$

WT is given in kg, DW in mm. The largest specimen in the sample was a female; DW was not measured because the fishermen had already started filleting the pectoral fins. Calculated DW, regressed from disc length, cranial width, and upper toothband length, was 1,801 mm (multiple correlation coefficient = 0.99). The second largest specimen was also a female, 1,799 mm DW. The largest male had a DW of 1,770 mm and weighed 53 kg. The smallest freshly caught specimen was 876 mm DW and weighed 6.4 kg. The smallest postnatal specimen was a male, the carcass of which was found drying on the beach in Ensenada de los Muertos. Its calculated DW, regressed from toothbands length, was 864 mm (multiple correlation coefficient = 0.99).

Overall ratio of males to females caught was 1.18 (N = 148). Catch sex ratios varied with season. Females appeared to be dominant in winter (ratio of males to females 0.27; N = 14). The reverse was true in March, in favor of males. A significant difference from a 1:1 ratio (chi square test $P > 0.05$) was not noted. Geographical segregation, either of sex or size, was not apparent for *M. thurstoni* during the warmer months when a wide array of size classes and both sexes were found in the same fishing area. Males and females were occasionally harpooned from the same group basking at the surface. This fact argues against behavioral sex segregation. Winter data, however, were suggestive of size segregation at that time of year. It was common knowledge among local fishermen that during the winter months all *M. thurstoni* caught are small. The bimodal size-frequency distribution for early

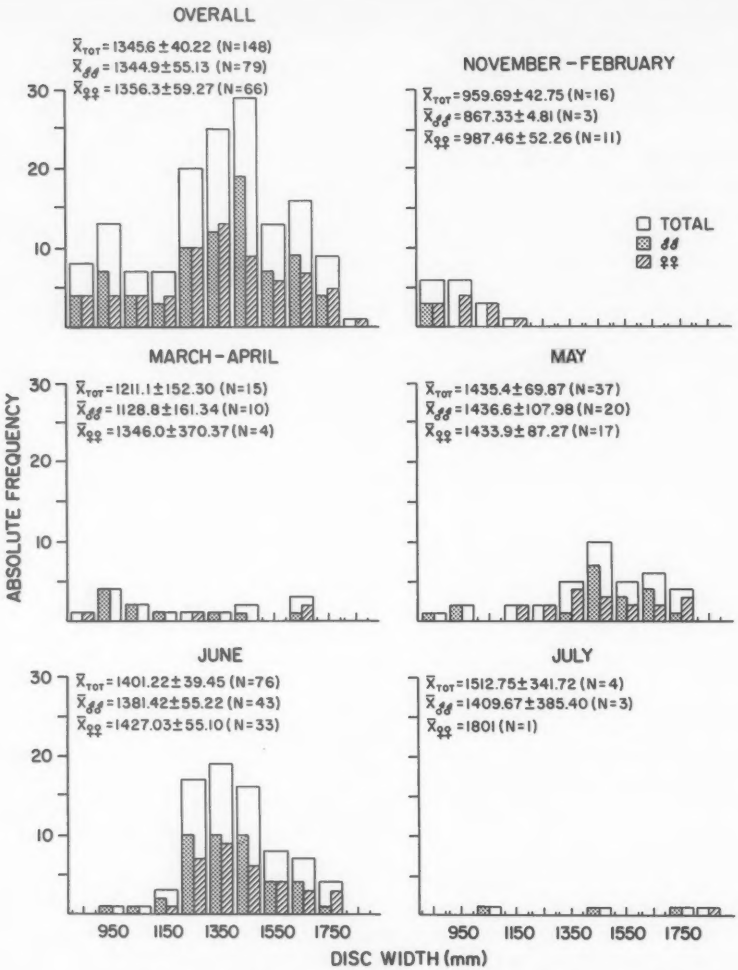

FIGURE 2.—Size-frequency distributions of *Mobula thurstoni* (means ±2 SE).

sprin g (Fig. 2) suggested that larger rays began to move into the area in the spring from their unknown wintering grounds.

Mature testes are large, elongated structures attached by the mesorchia to the upper anterior wall of the pleuroperitoneal cavity, on either side of the vertebral column. A large epigonal organ is associated with each testis. Both testes appeared to be functional. They were usually about the same size, although occasionally the left testis was nearly 25% larger. The paired ducti deferentes remain separated from each other throughout their length and open into the cloaca at the tip of the urogenital papilla through two distinct pores, rather than merging in the urogenital sinus, as in most elasmobranchs (Daniel 1934), including *Manta ehrenbergi* (Gohar and Bayoumi 1959). Clasper length was plotted against DW for 43 *M. thurstoni* (Fig. 3), to determine the onset of male maturation. Rapid increase in relative size of the claspers, beginning at a DW of about 1,500 mm, was concomitant with the incipient presence of abundant seminal fluid in the lower portion of each ductus deferens. The pelvic fin area, and

especially the tissue at the bases of claspers, of the larger males appeared swollen and congested in May and June, and some of the skin had assumed a pink coloration. Similar observations in carcharhinid and odontaspid sharks have been linked with mating activities (Springer 1960; Gilmore et al. 1983).

The ovaries in *M. thurstoni* are paired, elongated organs located inside the pleuroperitoneal cavity, analogously to the testes, and are connected to a large epigonal organ. Eggs are produced within the germinative epithelium. The largest eggs were found at the anterior end of the ovary. Only the left ovary develops and is functional, whereas the size and aspect of the right ovary remains comparable with those of the immature stage. Asymmetry is also present in the oviducts, the left uterus being usually the largest in mature females. It consists of a voluminous, thick-walled expansion of the lower tract of the oviduct; its lumen is lined with a highly developed epithelium consisting of elongated, flattened villi (trophonemata), a well-known mobulid (Gill 1908; Setna and Sarangdhar 1950; Wourms 1977) and rhinopterid (Schwartz 1966; Smith and Merriner 1986) feature. In several instances both uteri were found to contain a viscous, whitish or greenish substance. Oviducts open separately into the cloaca. A progression of sexual maturity in female mobulids was evident from the examined ovary's developmental condition. In the immature female the germinative epithelium is a narrow, leaf-shaped band, tapering at both ends, located opposite to the mesovarium (facing the center of the cavity) along the ovary's longitudinal axis. In mature females the germinative epithelium takes over most of the ovary's ventral side, making room for the mature ova. To determine the size at maturity of female *M. thurstoni*, the diameter of the largest ovarian egg was plotted against DW (19 specimens, Fig. 4). An egg growth plateau was not evident, because data on

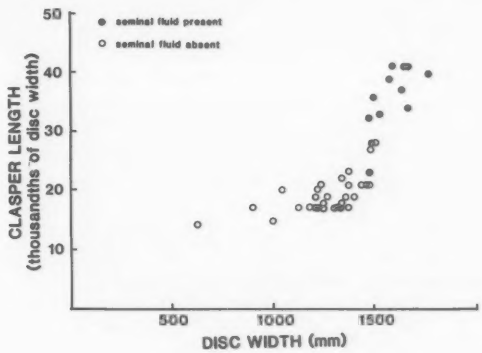

FIGURE 3.—Relationship between clasper size and body size in *Mobula thurstoni*.

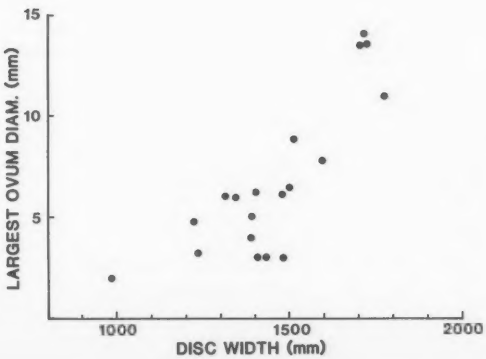

FIGURE 4.—Relationship between size of largest ovum and body size in *Mobula thurstoni*.

the larger sizes were insufficient, and therefore the maximum egg diameter was not known. It appears from the scanty available data that female *M. thurstoni* began to mature at a DW of about 1,500 mm (the point at which the slope of the curve becomes steeper).

Mobula thurstoni, like all mobulids, is a viviparous matrotroph (Wourms 1981), the near-term embryo being three orders of magnitude larger than the mature egg. Uteri and nidamental glands of 68 females were inspected. No adult female examined from March through June (N = 55) was pregnant. Embryos were found in July and October. Two embryos from females caught in July were near-term. Four embryos found in October were in an early stage of development. All females (N = 4) inspected in October were pregnant, and all embryos were in the same developmental stage, suggesting coordinated breeding activity. The largest female (DW 1,801 mm) had a single embryo, which appeared to be in the final stage of fetal development, fully pigmented, the yolk sac completely absorbed, and the umbilicus a mere scar (Fig. 5A). The embryo's DW was 630 mm; its WT, 3.4 kg. It occupied the left uterus with the rostrum pointed forward. Its pectoral fins were folded dorsally, the right pectoral on top. The cephalic fins were almost totally unrolled and extended ventrally towards the midline of the body. The uterus, with the embryo inside, occupied roughly one third of the female's pleuroperitoneal cavity. Lack of space inside the cavity and the distended skin on the abdomen made it apparent that no other embryo had been recently expelled or aborted. Uniparity appears to be a common pattern within the genus *Mobula* (Hill 1862; Gill 1908; Coles 1913, 1916b; Barnard 1925; Setna and Sarangdhar 1950; Cadenat 1960; Wallace 1967; Capapé and Zaouali 1976; Figueiredo 1977). Only Risso (1826) asserted that *Cephaloptera giorna* (= *M. mobular*) may have one or two young, but his statement was not documented. Since the smallest free-swimming specimen noted had a DW of 864 mm, the average size at birth for *M. thurstoni* is probably between 650 and 850 mm DW, and a WT of approximately 4.5 kg. The second largest female (DW 1,799 mm) had also only one embryo in her left uterus. The embryo was unpigmented, with disc 210 mm wide, and weighed 173 g. Like the term-embryo, its rostrum was pointing forward; unlike it, however, its pectoral fins were folded ventrally.

Mating, parturition, and early mobulid life history take place in the shallower portion of a population's range, not an uncommon elasmobranch feature. McLaughlin and O'Gower (1971) discussed inshore movements in the mating Port Jackson shark *Heterodontus portusjacksoni*, as did Springer (1960) for the sandbar shark *Eulamia milberti* (= *Carcharhinus plumbeus*). One-year-old gray reef sharks, *Carcharhinus amblyrhynchos*, were observed in French Polynesia in shallower waters than adults by Nelson and Johnson (1980). A similar result was reported for the hammerhead shark, *Sphyrna lewini*, by Clarke (1971) in Hawaii and by Klimley (1983) in the Gulf of California. Bullis (1967) hypothesized an upward movement to shallower depths for newborn marbled cat sharks, *Galeus arae*. There is likely an advantage for juveniles to remain in relatively protected areas during the earlier stages of their life, when they are most vulnerable to predation (Springer 1967).

Examination of 139 stomachs indicated that *M. thurstoni* was extremely specialized in its feeding habits. Eighty one (58.3%) stomachs were empty, or had only traces of food (<1 g wet weight). The remaining 58 stomachs (41.7%) had quantifiable contents. All recognizable prey items were planktonic crustaceans (with the exception of a few fish eggs, one nematod, and a small coleopteran, probably ingested accidentally when it was floating). They were listed, ranked by decreasing %IRI, in Table 1. *Mobula thurstoni*

TABLE 1.—Prey species found in 57 stomachs of *Mobula thurstoni*, ranked by decreasing Index of Relative Importance (IRI). N = percentage of prey species by number; M = percentage of prey species by mass; F = percent frequency of occurrence of prey species.

Prey species	N	%N	M	%M	%F	IRI	%IRI
Nyctiphanes simplex	4,940.8	86.70	4,982.0	87.40	87.7	15,268	97.90
Mysidium sp.	635.2	11.10	631.2	11.10	12.3	273	1.75
Copepoda	99.9	1.80	74.5	1.31	15.8	49	
Megalopa larvae	12.0	0.21	4.1	0.07	14.0	3.95	
Hyperiid amphipods	6.8	0.12	5.8	0.10	5.3	1.18	0.35
Fish eggs	1.4	0.03	1.8	0.03	5.3	0.302	
Nematoscelis diff.	0.5	0.01	1.1	0.02	1.8	0.050	
Stomatopod larvae	0.7	0.01	0.6	0.01	1.8	0.041	

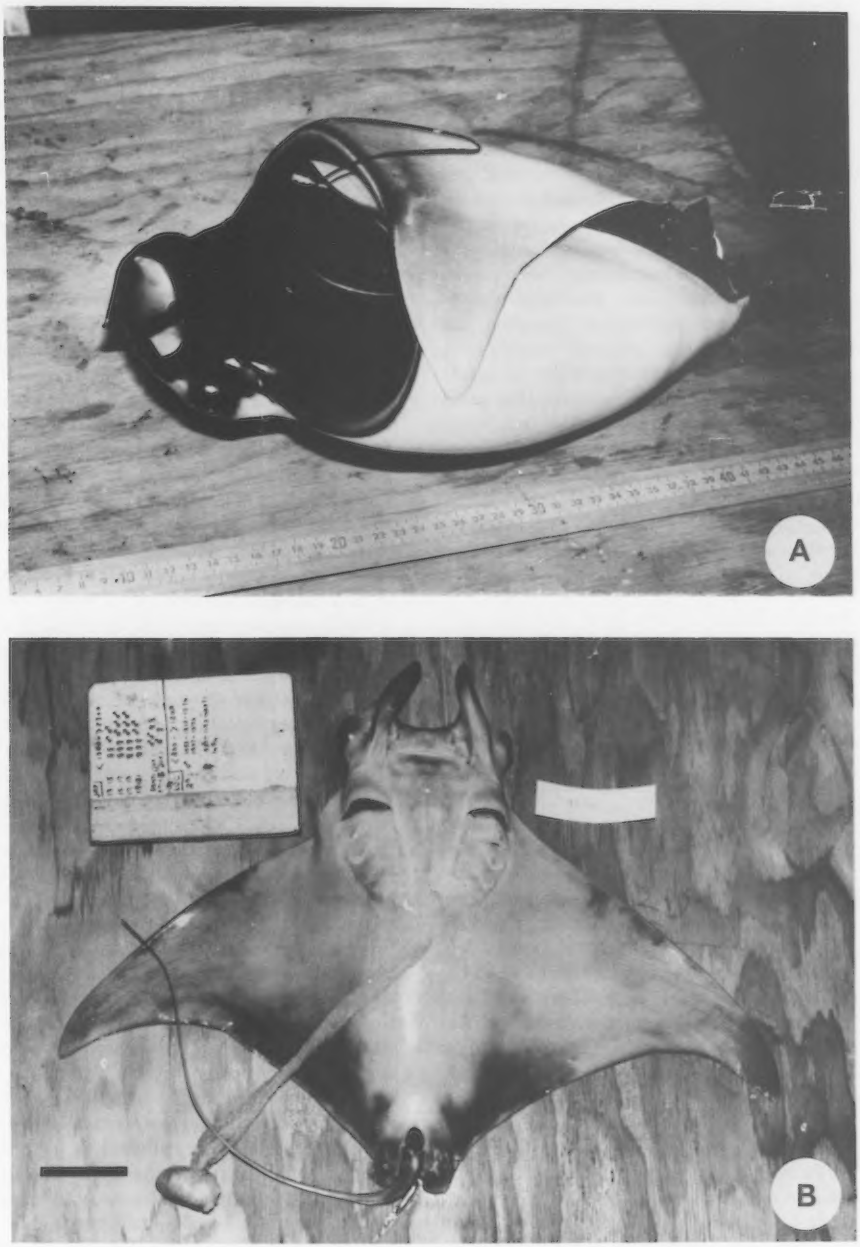

FIGURE 5.—A: term-embryo of *Mobula thurstoni*. The scale in the photograph is in centimeters. B: embryo of *M. tarapacana*. The scale bar equals 5 cm.

fed mostly on adult and juvenile euphausiids, *Nyctiphanes simplex*. The mysid *Mysidium* sp. (underscribed, Thomas E. Bowman[2]) was second in order of importance. Mysids and euphausiids were never found together in the same stomach. The overall importance of the two food items differed by two orders of magnitude. All other prey species found in the stomachs were rare and probably fortuitously ingested. These included one zoea larva and the following copepod species: *Undinula vulgaris*, *Eucalanus subcrassus*, *E. subtenuis*, *Temora discaudata*, *Scolecithrix danae*, *Nannocalanus minor*, *Euchaeta remana*, *Euchaeta* sp., and *Labidocera diandra*. Diet varied with season (Fig. 6A), with mysids being dominant from December through March, and euphausiids during the warmer months. Diet varied with predator size (Table 2): smaller individuals fed both on euphausiids and mysids; the larger rays fed only on euphausiids. This result probably reflects the predominance of smaller rays during winter, when fewer euphausiids are available, rather than an ontogenetic change in food preferences.

TABLE 2.—Size differences in the diet of *Mobula thurstoni*.

	%IRI	
Prey species	DW < 1,300 mm (n = 21)	DW > 1,300 mm (n = 36)
Nyctiphanes simplex	79.04	99.91
Mysidium sp.	18.13	0
Other	2.83	0.09

Two remoras (Echeneididae) were occasionally found on large *M. thurstoni*: *Remora remora* (3 specimens; range: 98–200 mm SL), and *R. albescens* (3 specimens; 93–100 mm SL). Crustacean parasites were encountered: *Pupulina minor* (Copepoda: Caligidae), *Ecthrogaleus denticulatus* (Copepoda: Pandaridae) sparsely on the skin, and *Ecthrogaleus disciarai* (Benz and Deets 1987) in large patches on the dorsal surface, *Entepherus laminipes* (Copepoda: Cecropidae) from the branchial filter plates, *Eudactylina oliveri* (Copepoda: Eudactylinae) from the gill lamellae, and *Kroeyerina* sp. (Copepoda: Kroyeriidae) from the olfactory lamellae.

Mobula thurstoni was usually observed at the surface in coastal waters of Bahia de la Ventana, Cueva de Leon, and Bahia de los Muertos, often within a few hundred meters of land and occasionally as far as 6 km. When sighted offshore, it was sometimes found over considerable depths (>500 m), although it appeared to be more abundant in shallower, neritic waters. *Mobula thurstoni* was always caught in the shallower part of the nets, usually at a depth of <100 m. The greatest part of the catch, however, was surface-dwelling rays. Beginning in mid-April, numerous *M. thurstoni* were consistently seen in the early morning hours cruising slowly at the surface. They would frequently pause, conspicuous on calmer days, with the tips of their pectoral fins protruding out of the water. This behavior is well known in mobulids (Norman and Fraser 1937); it has been observed also in connection with mating activities in *M. olfersi* (= *M. hypostoma*) by Coles (1910). During such occasions, fishermen could easily approach the rays and harpoon them, before startling them and causing them to dive. Repeated captures within the same aggregation revealed that rays of various sizes and both sexes could be found together. While at the surface, *M. thurstoni* was usually solitary or in small, nonpolarized groups (2–6), rather than in larger aggregations or schools. The species was frequently seen jumping out of the water in spectacular, often reiterated somersaults; it was recognized by the distinctive ventral markings.

It is not known to what extent mobulids make use of the sea bottom. Beebe and Hollister (1935) observed a group of 12 small devilfish (most likely *Mobula*) lying on the sandy substrate off Frigate Islet, in the British West Indies. Bigelow and Schroeder (1953) speculated that *Manta* spends much of its time resting quietly on the seafloor. During an experiment organized in conjunction with Sea World of San Diego, aimed at establishing whether *M. thurstoni* could survive in a confined environment, five young specimens were captured with gill nets and kept in a large pen (6 m in diameter) anchored in 2.5 m of water in Ensenada de los Muertos. None of the rays survived 24 hours of captivity; the reasons for their deaths were not clear, although the particularly stressful capturing method appeared as a likely cause. During that experiment the negatively buoyant rays (sinking tail-first as soon as they stopped swimming) spent a great deal of time resting on the bottom, and were able to circulate water through their gills while resting, by a synchronized maneuvering of the oral valve and of the gill covers (as judged from the flow made visible by the numerous particles suspended in the water). A frequent method of turning around

[2]Thomas E. Bowman, Smithsonian Institution, Washington, D.C., pers. commun. 1984.

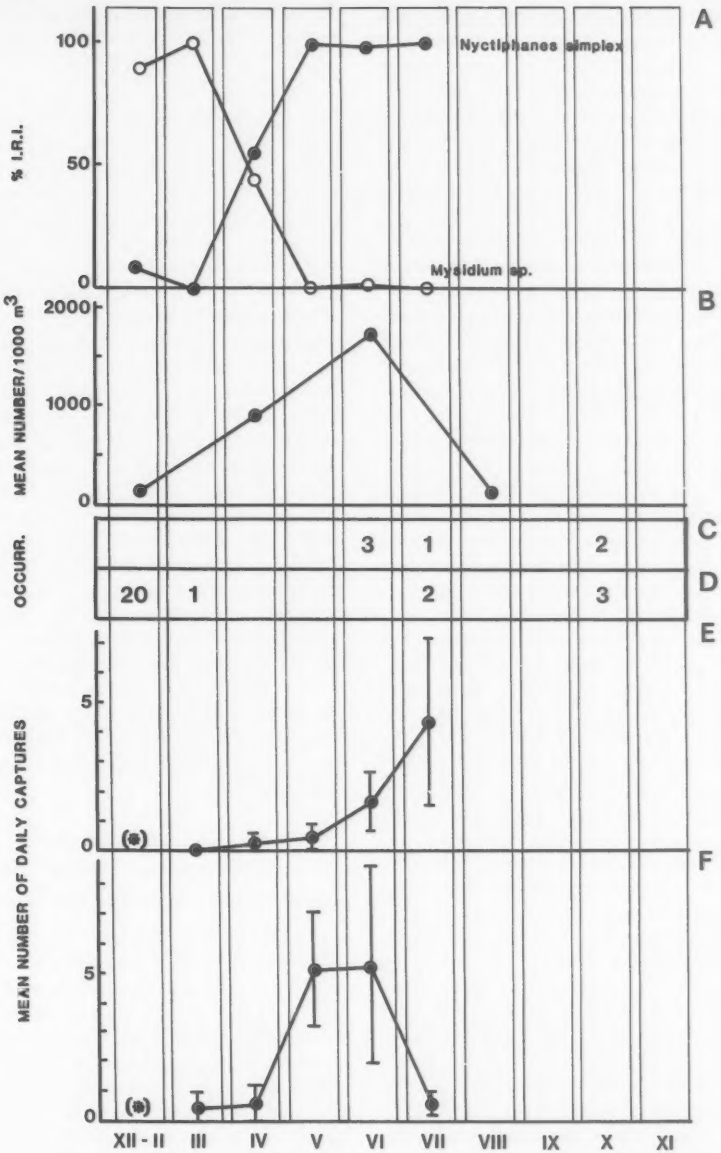

FIGURE 6.—A. seasonal variation of the relative importance of *Nyctiphanes simplex* and *Mysidium* sp. in the diet of *Mobula thurstoni*. B. seasonal variation of the abundance of adult and juvenile *N. simplex* in the coastal areas of the southwestern Gulf of California (modified from Brinton and Townsend 1980). C. captures of *M. tarapacana*. D. captures of *M. munkiana*. E. mean number of daily captures of *M. japanica*; bars represent 2 SE on either side of the mean. F. mean number of daily captures of *M. thurstoni*; error bars as in E. (*): although specimens were also captured between December and February, data are not comparable with spring and summer captures because catch effort was minor and inconsistent in the colder months.

(e.g., when swimming towards the wall of the pen) was to dive vertically in a tight circle until swimming in the opposite direction in an inverted position, and then spinning around the body axis to bring the dorsal side up, rather than turning by banking to the right or to the left.

An indication of the seasonal abundance of *M. thurstoni* in the surface waters of the study area was obtained by the mean number of rays caught daily from March to July 1983 (Fig. 6; Table 3). Mean daily catch should be taken as a rough indication of the relative abundance of *M. thurstoni* rather than as a precise index because the fishing effort was difficult to quantify. Mean effort, however, was roughly constant from March through July because the mean monthly number of working boats (about 20) and the number and size of the nets set then was constant. Furthermore, the fishermen would harpoon a ray every time they had the opportunity to do so. Peak of abundance was in June, a result which appears to be consistent with the fishermen's past experience, despite the 1983 abnormally high water temperatures (Cane 1983). In July the number of *M. thurstoni* caught had dropped drastically, and most of the catch consisted of *M. japanica*. No information was obtainable for the August–September period. Eighteen specimens were captured during six fall and winter field trips (24 January–8 February 1981; 25 November 1981; 16–21 December 1981; 20–23 December 1982; 19–26 January 1984; 28 October–1 November 1984), but that figure was not comparable with other data because part of the fishing cooperative migrated south to Los Frailes during the cooler months. It is common knowledge, however, among the local fishermen, that *M. thurstoni* in the colder season is present, but in fewer numbers than during the summer.

The study area constitutes a feeding, mating and nursery ground for *M. thurstoni*. The euphausiid *Nyctiphanes simplex*, the main diet item and the only food of the adults when in the area, is the most abundant and widespread euphausiid in the Gulf of California, and has been observed in dense swarms (Brinton and Townsend 1980). Although it is found in the study area year-round, its juvenile and adult stages are most abundant between February and August, peaking in June on the west side of the Gulf of California (Brinton and Townsend 1980). The seasonal abundance of *M. thurstoni* in the southern Gulf thus seems to be closely related to the seasonal abundance of its main prey. It is impossible to describe the general movement and life history pattern of *M. thurstoni* in the Gulf of California from the fragmentary information available. The scanty data, however, suggest the following: 1) adult male and nonpregnant adult female *M. thurstoni* enter the area in spring to feed and to mate, 2) pregnant females segregate from the rest of the population in spring (as is also suggested by the slight predominance of males in spring and early summer), 3) gestation period is one year and females give birth to one young every two or more years, 4) the young are born in the study area or near it in midsummer and remain there throughout their early life, and 5) in late summer, when the numbers of adult and juvenile *Nyctiphanes simplex* decline due to intense heating of the water (Brinton and Townsend 1980), adult *M. thurstoni* leave the area, whereas the young switch their diet from euphausiids to mysids. Further investigations are needed for additional corroboration of these hypotheses.

TABLE 3.—Mean number of daily captures of *Mobula thurstoni*. a = total monthly number of captures; b = monthly number of days of monitoring; $\overline{X}$ = mean number of daily captures; SE = standard error of the mean; SD = standard deviation.

Month	a	b	$\overline{X}$	2SE	SD	range
March	6	16	0.38	0.54	1.1	0–4
April	9	13	0.69	0.69	1.3	0–4
May	35	7	5.00	1.95	2.6	1–9
June	77	15	5.10	3.32	6.4	0–23
July	5	9	0.56	0.34	1.0	0–3

Mobula japanica (Müller and Henle 1841) Local name: cubana de lomo blanco

A total of 78 specimens, 34 males (DW range 1,316–2,386 mm) and 44 females (1,470–2,302 mm), were caught at three stations (Punta Arena de la Ventana, Cueva de Leon, and Ensenada de los Muertos) and adjacent waters, between 16 December 1981 and 13 July 1983. Overall and seasonal size-frequency distributions for *M. japanica* are shown in Figure 7. With the exception of April, when females were larger (T-value = 4.697, df = 3, $P < 0.02$), there are no significant size differences between the sexes (T-value = 0.535, df = 76, $P > 0.5$). Most of the rays in the sample were large; only three were <1,900 mm DW.

Twenty-seven specimens (size range: 1,316–2,285 mm DW; 18.6–115 kg) were weighed. The WT/DW relationship is described by the equation:

$$WT = 4.29 \times 10^{-10} (DW)^{3.4}$$

$$r = 0.98$$

where WT is given in kg, DW in mm. The overall male to female ratio was 0.89 ($N = 78$). Females dominated the June through December period; males were predominant in April and May. Sex ratios, however, never significantly differed from 1 (χ^2 test $P > 0.05$). Sex segregation, behavioral or geographical, was never observed in *M. japanica* (both sexes were caught together in nets and by harpoon); sampling bias ($N = 3$) may explain why only males were caught in May. Geographical size segregation, by contrast, was an evident feature of sexually mature specimens in the Gulf of California (Fig. 7).

No pregnant females were found, although in some specimens the left uterus had a flabby and dilated appearance, suggesting recent delivery. Tissues at the base of the claspers of most of the larger males were swollen and reddened in June and July when the tips of the claspers were flexible and the rhipidion could be easily spread, and in doing so a white, viscous fluid would ooze from the hypophyle; all this suggested mating activity. The clasper length-DW relationship for *M. japanica* (Fig. 8) did not exhibit a clear pattern as in *M.*

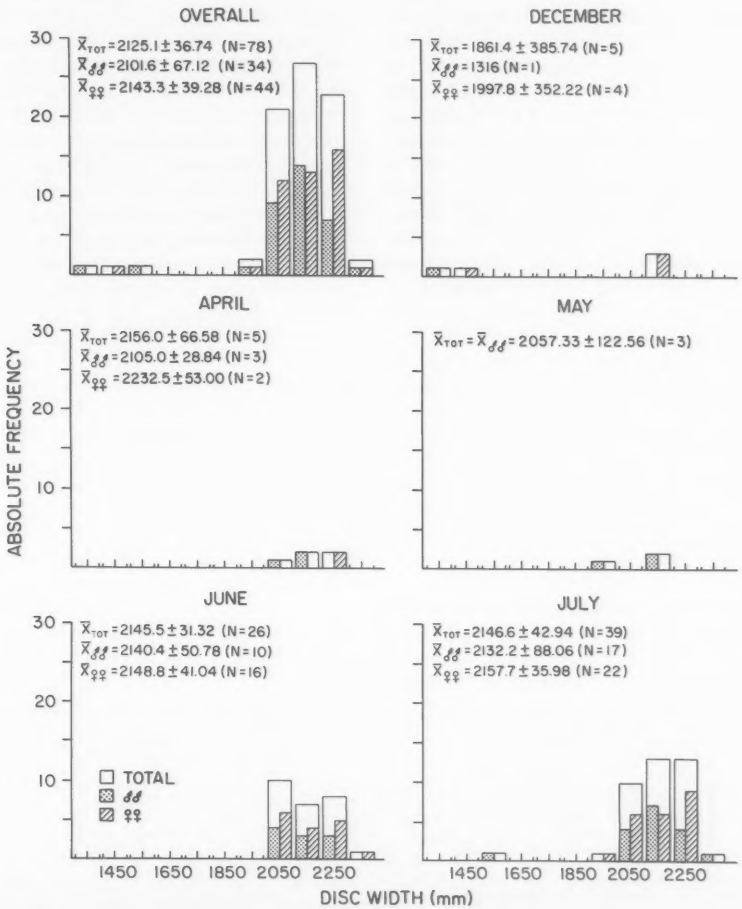

FIGURE 7.—Size-frequency distributions of *Mobula japanica* (means ±2 SE).

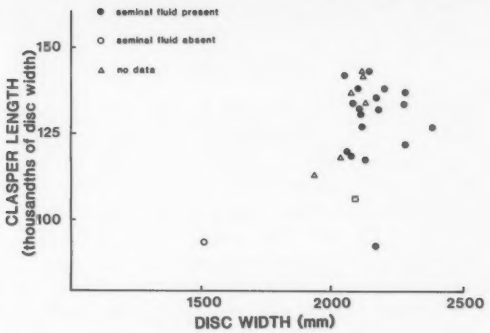

FIGURE 8.—Relationship between clasper size and body size in *Mobula japanica*.

thurstoni, since most of the specimens of *M. japanica* were of larger size classes. It was apparent, however, that at a DW between 2,050 and 2,150 mm there is a high degree of variability in the relative size of claspers, which tended to stabilize at higher values (DWs >2,150 mm), indicating that male sexual maturity in *M. japanica* begins at a DW of 2,100 (±50) mm. Lack of information on smaller specimens prevented a clear understanding of the onset of female sexual maturity (Fig. 9). Large eggs were found in specimens as small as 2,070 mm DW, possibly indicating that female *M. japanica* began to mature at that size.

Only 19 (24%) of 78 specimens had quantifiable stomach contents (>1 g wet WT). The remaining 59 stomachs (76%) were empty or had only traces of food. All *M. japanica* fed largely on the euphausiid *Nyctiphanes simplex* (Table 4); no mysids were found. Other species occurring in the stomachs, including copepods, megalopa larvae, stomatopod larvae, hyperiid amphipods, caridean decapods (*Crangon* sp., *Pasiphaea* sp., and one alpheid decapod), and one cumacean, had an overall relative diet importance of only 0.38%. *Mobula japanica* were therefore very similar in feeding habits to large *M. thurstoni*. Information on the

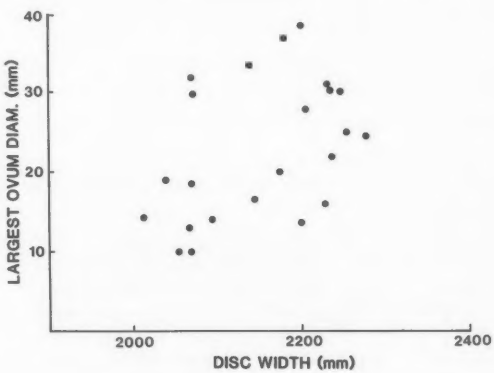

FIGURE 9.—Relationship between size of largest ovum and body size in *Mobula japanica*.

TABLE 4.—Prey species found in 19 stomachs of *Mobula japanica*, ranked by decreasing Index of Relative Importance (symbols as in Table 2).

Prey species	*N*	%*N*	*M*	%*M*	%*F*	IRI	%IRI
Nyctiphanes simplex	1,890.64	99.51	1,869.85	98.41	100.00	19,792	99.62
Copepoda	4.61	0.24	1.15	0.06	31.58	9.47	0.05
Other	4.74	0.25	29.00	1.53	36.84	65.58	0.33

winter diet of *M. japanica* was lacking, as four of the five specimens collected then had empty stomaches; the fifth, a large female, contained a small fragment of a partially digested fish carcass. Since quantifiable stomach contents were found only in large rays between April and July, no size or seasonal differences in the diet of *M. japanica* could be detected.

Mobula japanica was often found carrying *Remora remora*, usually seen clinging to the outside of body, but found once inside a spiracle. Six specimens of *R. remora* (range 109–217 mm SL) were collected from *M. japanica*. Only one specimen of *R. albescens* (97 mm SL) was found, in the mouth cavity of a *M. japanica*. A pilot fish, *Naucrates ductor* (Carangidae) also associated with *M. japanica*, swam alongside a harpooned ray that was being towed inshore and remained for some time at the water's edge, where the ray was beached. *Mobula japanica* was parasitized by the following crustaceans: *Nerocila acuminata* (Isopoda: Cymothoidae), *Pupulina brevicauda* and *P. minor* (Copepoda: Caligidae) on the skin; *Eudactylina oliveri* (Copepoda: Eudactylinae) in the gills; and *Kroeyerina* sp. (Copepoda: Kroyeriidae) among the olfactory lamellae. Unidentified trypanorhynch cestodes were occasionally found within the pleuroperitoneal cavity.

Habitat preference of *M. japanica* did not appear to differ from that of *M. thurstoni*. However, the use of the habitat differed seasonally: in April and May, when *M. thurstoni* was abundant at the surface, *M. japanica* was never seen, and few specimens were bottom gillnetted during those months. Conversely, *M. japanica*, in June and July, was seen in the late morning hours at the surface in groups of several individuals swimming parallel to the shore. Occasionally specimens were seen in water <1 m deep. *Mobula japanica* is not known to school, and I never observed schooling.

Coles (1910) reported that *M. olfersi* (= *M. hypostoma*) utters a "musical, bell-like bark" when dying. A similar account was given by Risso (1810) of *Cephalopterus massena* (= *M. mobular*). This information led subsequent authors (Norman and Fraser 1937; Bigelow and Schroeder 1953) to wonder whether mobulid rays are capable of producing sounds while in the water. Sound production is a fairly widespread phenomenon among bony fishes (Fish and Mowbray 1970; Tavolga 1971); however, elasmobranchs lack the traditional structures used by teleosts to generate sound, i.e., the swim bladder and bony skeletal parts (Marshall 1962), and recognizable sounds have not been recorded from these animals (Backus 1963). Sound production among elasmobranchs has been reported only for the Atlantic cownose ray, *Rhinoptera bonasus* (Myrberg 1981); in that case clicks and scraping sounds were presumably produced with the dental plates, elicited when strongly prodding three rays which were confined in a tank (Fish and Mowbray 1970). *Mobula japanica*, when beached alive, often emitted a distinctive noise which could have been the equivalent of Coles' "bark". This noise, however, was apparently caused by the periodic, spasmodic contractions of the mandibular, pharyngeal, and hypobranchial musculature of the asphyxiating ray, which forced air from the mouth cavity out of the gill openings through the meshlike branchial filter plates. Although underwater sonic recordings have never been made, it seems unlikely that under normal circumstances any audible sound could be produced in this fashion by submerged mobulids.

This area served as a spring and summer feeding and mating ground for adult *M. japanica*, rather than as a pupping or nursery ground, as indicated by the lack of small-sized specimens. Seasonal abundance of *M. japanica* in the surface waters was indicated by the catch data (Table 5) and is comparable to the seasonal abundance of *M. thurstoni* (Fig. 6). No *M. japanica* were observed in March; in April and May they occurred occasionally. By mid-June large numbers appeared in the nearshore surface waters near Punta Arena de la Ventana, and were easily harpooned. Most of the July mobulid catch consisted of *M. japanica*, when the numbers of *M. thurstoni* had declined. Data are lacking for the August–October period, therefore it was impossible to tell whether the peak of abundance occurred in July or later. Fishermen's reports were not clear, although there was agreement on an overall decline of mobulid abundance in late summer. *Mobula japanica* fed exclusively on the euphausiid *Nyctiphanes simplex*, and its numbers apparently declined concomitant with the late summer decline

TABLE 5.—Mean number of daily captures of *Mobula japanica* (symbols as in Table 1).

Month	*a*	*b*	$\bar{X}$	2 SE	SD	range
March	0	16	0	0	0	0–0
April	5	13	0.4	0.36	0.7	0–2
May	3	7	0.4	0.40	0.5	0–1
June	26	15	1.7	1.02	2.0	0–6
July	39	9	4.3	2.89	4.3	0–14

of abundance of their prey (Brinton and Townsend 1980). Some *M. japanica*, however, including individuals both large and small, were found in this region throughout December. Like *M. thurstoni*, winter catch data are not comparable because of differences in fishing effort, when *M. japanica* is apparently caught less frequently.

Mobula munkiana Notarbartolo-di-Sciara 1987 Local name: tortilla

Twenty-four specimens, 10 males (DW range 686–900 mm) and 14 females (719–1,097 mm), were caught at four stations (Punta Arena de la Ventana, Ensenada de los Muertos, Bahia de los Frailes, and Isla El Pardito) and adjacent waters, between December 1982 and October 1984. Size-frequency distributions for *M. munkiana* (Fig. 10) revealed that female mean size was greater than male, although not significantly (T-value = 1.724, df = 22, $P > 0.1$). Seasonal differences in size-frequency distribution could not be examined because *M. munkiana* were only collected during the fall and winter. All 10 freshly captured specimens were weighed (size range: 686–1,097 mm DW; 4.1–11.8 kg). Their WT/DW relationship is described by the following equation:

$$WT = 1.041 \times 10^{-6} (DW)^{2.34}$$

$$r = 0.95.$$

WT is given in kg, DW in mm.

The largest specimen in the sample, a female, was one of the largest "tortillas" ever seen. There are no data on size at birth, as no embryos were found. Lack of knowledge of the size of the young of the year also prevented insight on size segregation. Term-embryos in *M. rochebrunei*, a closely related, similar sized species from west Africa, were 340–350 mm wide (Cadenat 1960). Since *Mobula* at birth has a DW of about 1/3 of the adult, size at birth would be about 350 mm DW. This information argues in favor of size segregation in *M. munkiana*. Male to female ratio was 0.71 ($N = 24$), insignificantly different from 1 (χ^2 test $P > 0.05$). Both sexes were caught in the same net sets, indicating that males and females school together, and that there was no sex segregation, either geographic or behavioral.

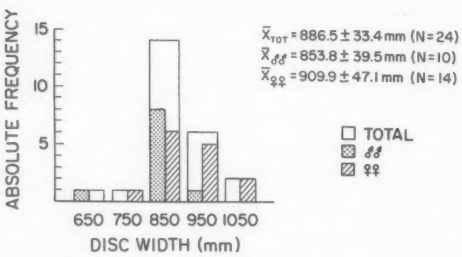

FIGURE 10.—Size-frequency distributions of *Mobula munkiana* (means ±2 SE).

A dried, twisted male carcass, for which morphometrics could not be obtained, with a calculated DW of 895 mm, had long, well-developed claspers, markedly protruding beyond the pelvic fins. Based on other mobulid species, this condition indicates sexual maturity. A second specimen, with a disc 686 mm wide, had small and pliable claspers, and the ratio between clasper length and pelvic fin length, both measured from tip to anterior margin of vent, was 0.88. At this ratio, both *M. thurstoni* and *M. japanica* are immature. Two *M. munkiana*, 871 and 872 mm DW, differed greatly in the relative size of their claspers: one possessed slightly longer claspers than the pelvic fins (ratio = 1.10), and an incipient hardening of the cartilage was apparent; in the other specimen the claspers were much shorter than the pelvics (ratio = 0.84), and still soft. This information suggested that male sexual maturity in *M. munkiana* began at about 870 mm DW.

The largest female specimen was sexually mature, as it had a large, flaccid left uterus, and the enlarged left ovary consisted mainly of about 30 macroscopic ova (size range 2–15.2 mm).

Ten stomachs were examined: four were empty, three contained unidentifiable whitish matter, and three were full of planktonic crustaceans. A list of prey species ranked by decreasing %IRI is given in Table 6. *Mysidium* sp. appeared to be the main staple of *M. munkiana*'s diet. *Mobula munkiana* is thus similar to the wintering young of *M. thurstoni*. One of the stomachs contained coarse coral fragments and small gastropod shells, perhaps ingested by the ray while foraging on mysids near a sandy substrate. The west African species *M. rochebrunei* appeared to have similar feeding habits, as Cadenat (1960) found mysids and a few larger postlarval stomatopods in the stomachs of several specimens.

I have no record of remoras associating with *M. munkiana*. The only parasitic crustacean

found was *Pupulina* cf. *minor* (Copepoda: Caligidae) from the skin.

Among *M. munkiana*'s distinguishing features are its neritic preferences combined with its social habits. This is the only mobulid species in the Gulf of California that was consistently seen in schools. It is not known whether this is a seasonal behavior, or a permanent ethological feature of the species. Schools appear as a conspicuous dark patch, sometimes a few tens of meters in diameter, as they slowly cruise along the coastline in shallow water. The presence of the school is often also highlighted by the frequent, simultaneously leaping individuals, which betray its position from a long distance. Similar behavioral traits (schooling and leaping) have been reported for two closely related species from the Atlantic, *M. hypostoma* (Bancroft 1829; Coles 1910, 1916a) and *M. rochebrunei* (Cadenat 1960). During leaps, *M. munkiana* occasionally reached a height of about two DWs. Two types of leaps were observed: rising vertically head first and landing flat with the belly on the sea surface with a loud clap (breach), and spinning one to three times around the main transverse body axis (somersault).

A salient feature of *M. munkiana*'s ecology in this area is its winter occurrence when all other mobulids are absent or at their lowest numbers. *Mobula munkiana* apparently subsists then chiefly on the mysid shrimp, *Mysidium* sp., which is also the main food for young wintering *M. thurstoni*. However, *M. munkiana* frequents the area occasionally in summer: two specimens were caught by surface gill net in Bahia de la Ventana in July 1983. Even during the season in which it is most abundant, *M. munkiana* is seen in "pulses", as its occurrence at any particular location is spotty. It may occur in large numbers at one location for a few days, and then be absent for 1 or 2 weeks. This observation suggests the possibility that *M. munkiana* lives in large concentrations, perhaps composed by several schools, which travel along the coast. A similar phenomenon was observed off the Senegal coast by Cadenat (1960) in *M. rochebrunei*, a species which is closely related to *M. munkiana* both morphologically and ecologically.

It is conceivable that mobulids in the northern half of the eastern tropical Pacific mate and give birth in summer, based on the few term and near-term embryos found in summer in *M. thurstoni* and *M. japanica*, and from anatomical evidence of mating activity in adult males *M. thurstoni* and *M. japanica*. That such a hypothesis can also be extended to *M. munkiana* is supported by lack of reproductive activity in any of the specimens collected during the fall or winter, and that newborn and young-of-the-year are missing from the sample. This evidence corroborates the hypothesis that the local waters are a wintering ground for *M. munkiana*, which then migrates into an unknown area (perhaps the northern Gulf of California) during the warmer season for mating and pupping.

The possible causes of this ecological difference between *M. munkiana* and the other mobulids are many, and open to speculation. Mysid abundance may be declining in summer in the southern Gulf of California, and *M. munkiana* perhaps migrates to areas where this crustacean or related species abound during the warmer season. Alternatively, *M. munkiana* could be excluded from this region in spring by competition with the incoming, larger *M. japanica* and adult *M. thurstoni*. Finally, *M. munkiana* may be moving during the summer into an area which is more suitable for its reproductive needs. Unfortunately, this recently discovered species is very little known, and it has been reported only from the Gulf of California and Ecuador, although its distribution probably extends to other coastal areas of the tropical east Pacific (Notarbartolo-di-Sciara 1987).

TABLE 6.—Prey species found in three stomachs of *Mobula munkiana* ranked by decreasing Index or Relative Importance (symbols as in Table 2). Identifiable copepod species included *Undinula vulgaris*, *Rhincalanus nasutus*, and *Scolecithrix danae*. The stomatopods found were "erhithrus" larvae. One unidentified food item was a fragment of a larger crustacean, probably an euphausiid.

Prey species	*N*	%*N*	*M*	%*M*	%*F*	IRI	%IRI
Mysidium sp.	293.40	97.80	287.40	95.80	100.00	19,360	97.84
Stomatopod larvae	4.65	1.55	9.06	3.02	66.67	304	1.54
Copepoda	1.59	0.53	1.44	0.48	66.67	67.3	0.34
Other	0.37	0.12	2.10	0.70	66.67	54.7	0.28

Mobula tarapacana (Philippi 1892) Local name: vaquetilla

Mobula tarapacana is not a common species in the study area. Seven specimens were collected, one of which, a premature male embryo, was expelled by a large female while she was being landed. Of the postnatal individuals, two were male (DW range 2,476–2,494 mm), and four were female (2,704–3,052 mm). All were caught in Bahia de la Ventana between 9 June and 30 October 1983. All but two of the specimens were weighed. The following equation describes the WT/DW relationship for *M. tarapacana* (where WT is given in kg, DW in mm):

$$WT = 2.378 \times 10^{-8}(DW)^{2.92}$$

$$r = 0.998.$$

Although all sampled postnatal *M. tarapacana* were large, smaller individuals are known from the area, as can be seen in photographs taken at Punta Arena de la Ventana in summer 1981 (courtesy Felipe Galvan Magaña, CICIMAR, La Paz, Mexico; also Greg B. Deets[3]). This information argues against geographical size segregation of *M. tarapacana*. Data on the embryo provide no indication of size at birth, since it was still far from term. Pale pigmentation was apparent only around the head and pelvic regions, and the external yolk sac was present (Fig. 5B). The embryo, expelled tail first, was alive at birth. Judging by its size it had filled the left uterus completely and must have been the sole developing embryo.

The small size of the sample does not permit any clear inference on size at sexual maturity for *M. tarapacana*. Some indication, however, can be obtained by comparison with similar species. Of the two postnatal males, the specimen with a disc 2,476 mm wide appeared to be immature: no seminal fluid was found in the ducti deferentes, the testes were small and apparently little developed, and the ratio between clasper length and pelvic fin length was 0.94. Conversely, the second postnatal male, with a disc of approximately the same width (2,494 mm), possessed claspers longer than pelvics (ratio = 1.14), and the testes were well developed. Thus, sexual maturity in male *M. tarapacana* begins around a DW of 2,400–2,500 mm. The specimen with a DW of 2,704 mm, one of two nonpregnant females, had a bulky left ovary, containing numerous large eggs; the largest, 32 mm in diameter, weighed 12 g. Similar features appeared to be associated with sexual maturity in female *M. thurstoni* and *M. japanica*. The left ovary of another specimen, DW 2,831 mm, was smaller, and the diameter of the largest ovum was 18.6 mm, indicating that a DW of 2,700–2,800 mm denotes a transitional stage for female *M. tarapacana*, in which both mature and nonmature individuals can occur.

Twelve echeneidids were recovered from *M. tarapacana*. Three were *Remora remora* (size range: 108–229 mm SL), and nine were *R. albescens* (74–159 mm SL). The following crustacean parasites were also found: one cymothoid isopod (still in an unidentifiable aegathoid stage) and *Pupulina flores* (Copepoda: Caligidae) on the skin, *Entepherus laminipes* (Copepoda: Cecropidae) on the branchial filter plates, and *Eudactylina* sp. (Copepoda: Eudactylinae) in the gills.

Mobula tarapacana is strictly a summer and fall visitor to this region (Fig. 6C). This species is often found farther from the coast than *M. thurstoni* and *M. japanica*, and may have more pelagic habits. Four of the five stomachs examined (all from specimens caught in summer) were almost empty. Only traces of food were found among the folds of the stomach epithelium. Prey included four species of copepods (*Acartia* sp., *Pontella* sp., *Temora discaudata*, and *Undinula vulgaris*), hiperiid amphipods, one brachiuran (family Calappidae), one euphausiid, two caridean decapods (one of which belonged to the family Alpheidae), megalopa and stomatopod larvae, and a fish egg. The fifth stomach, from a late October capture, contained the remains of 27 fishes (probably carangids 15–30 cm long, and a smaller anchovy-like species). Small tetraodontids had been found before in the stomach of a *M. tarapacana* caught in Bahia de la Ventana (Felipe Galvan Magaña[4]). On this basis it is impossible to determine whether *M. tarapacana* is a specialized ichthyophagous ray, with the few crustacean items accidentally ingested while swimming, or a generalized feeder. The mesh size of this species' branchial filter plates is indeed greater than in other *Mobula* species (Notarbartolo-di-Sciara 1987). However, filter-

[3]Greg B. Deets, Long Beach State University, CA, pers. commun. 1984.

[4]Felipe Galvan Magaña, CICIMAR, La Paz, Mexico, pers. commun. 1983.

feeding on planktonic crustacea still appears to be a feasible foraging technique for *M. tarapacana*, judging from the size of its branchial sieve as it compares with the average-sized crustacean prey.

SUMMARY AND CONCLUSIONS

Four species of *Mobula* were found in the southern Gulf of California. The most abundant species, *M. thurstoni*, was present year-round, but only the smaller individuals were seen during the winter. The bulk of the population, including the adults, appeared in early spring. Numbers began declining in July. *Mobula japanica*, the second most abundant species, was comprised of only large individuals; numbers progressively increased from March throughout July. Large *M. japanica* were rare in winter, but were occasionally caught then. *Mobula tarapacana* is the rarest mobulid in the area, yet its presence as a summer and fall visitor is well known and predictable; it is believed by the local fishermen to be more abundant farther offshore. All three species share a similar pattern of peak summer seasonal abundance. The reverse is true for *Mobula munkiana*, it being most abundant in winter, and almost totally absent during the rest of the year. It is not known where any species goes when not seen in the area. Seasonal migrations within the epipelagic habitat to different areas of the Panamic region are likely, but unverifiable because of the present lack of knowledge of the occurrence of identified *Mobula* species south of the Gulf of California. Alternatively, devil rays may spend part of the year in midwater, or near the sea bottom, therefore disappearing from sight and reach.

There is a striking similarity between the array of mobulid species found in the Gulf of California (and probably along the Pacific coast of tropical America) and the mobulid fauna from the tropical waters off west Africa. The family is represented in both areas by *Manta birostris* and by four species of *Mobula*: *M. thurstoni*; *M. japanica* (reported from west Africa as *M. rancureli* by Cadenat 1959); *M. tarapacana* (reported as *M. coilloti* for African waters by Cadenat and Rancurel 1960 and Stehmann 1981); and a small gregarious form, represented in the Gulf of California by *M. munkiana* and off west Africa by the closely related *M. rochebrunei* (Notarbartolo-di-Sciara 1987). Tropical coastal areas off west America and west Africa are known to be among the most productive tropical waters in the world, because of comparable large-scale atmospheric and oceanographic circulation patterns (Sverdrup et al. 1942). It is conceivable that the ecological similarity between these two regions is reflected in similar faunal associations, especially as far as low levels of the tropic chain (e.g., plankton-feeding vertebrates) are concerned.

The Gulf of California presents a unique environment in the eastern Pacific Ocean, with extreme annual water temperature ranges, wind-induced mixing and upwellings, and subsequent great productivity (Roden 1964; Brusca 1980). Upwelling is caused along the peninsular coast by the southerly winds prevailing during the warmer months. This environment apparently creates optimal conditions for the existence of the euphausiid shrimp *Nyctiphanes simplex*, which is found in great abundance in the neritic habitat between spring and midsummer, before the intense August heat causes a decline in its numbers (Brinton and Townsend 1980). The following data are combined in Figure 6 to provide an overview of the possible relationship between the seasonality of predator and prey in the study area: a) the relative importance of *Nyctiphanes simplex* and *Mysidium* sp. in the diet of *M. thurstoni*; b) the relative abundance of *N. simplex*; the occurrence of *M. tarapacana* (c) and *M. munkiana* (d) in the catch; and the relative abundances of *M. japanica* (e) and *M. thurstoni* (f) (no data on the biology of *Mysidium* sp. are available).

Young *M. thurstoni* and all *M. munkiana* examined in winter appeared to subsist largely on *Mysidium* sp., whereas adult *M. thurstoni* and *M. japanica* caught during the warmer months fed exclusively on *N. simplex*. An extreme degree of feeding specialization was evident in all mobulid species in which quantitative analyses of the stomach contents was possible; most prey forms, other than *N. simplex* and *Mysidium* sp., were so rare that they were probably ingested accidentally. Stenophagy was linked to feeding specialization in another myliobatiform species, the mollusk-feeder *Rhinoptera bonasus* (Schwartz 1966; Smith and Merriner 1985). These results suggest that devil rays are highly efficient in locating and selecting their preferred food. They may be aided during this behavior by their prey's habit of swarming. Competitive interaction is to be expected between sympatric species-pairs which are closely related both taxonomically and ecologically. Food-resource partitioning is known to occur in sympatric species-pairs of skates

(McEachran et al. 1976). This condition, however, is not necessarily true when the sought-after resources are not in short supply (Zaret and Rand 1971). This may be the case of *M. thurstoni* and *M. japanica* feeding together on *N. simplex* when the abundance of euphausiids is at its peak. Competition should occur, however, in late summer, when prey numbers decline. It would be interesting to determine whether the slight morphological and behavioral differences between potentially competing species pairs (*M. thurstoni*/*M. munkiana* in winter, *M. thurstoni*/*M. japanica* in spring and summer) influence or reflect partitioning of their habitat when food resources become limiting, as was described for both freshwater (Werner and Hall 1977) and marine teleosts (Hixon 1980; Larson 1980).

This overview of the ecology and natural history of mobulids in the Gulf of California is based on field investigations made chiefly in 1983, a year in which the El Niño perturbation was particularly severe (Cane 1983). Although in terms of fishermen's experience the year 1983 was not unduly different, as far as mobulid relative abundance and seasonality are concerned, the abnormally high water temperatures resulting from El Niño may have affected the devil rays studied in subtle ways; therefore this investigation should be repeated in a normal year.

According to the fishermen, the abundance of sharks (mostly carcharhinids and sphyrnids) on which their activity is based is declining. This decline will probably result in an increase of mobulid fishing effort. It is of concern that 72% of the specimens of *M. thurstoni* caught were immature (DW <1,500 mm).

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NOTES ON DECAPOD AND EUPHAUSIID CRUSTACEANS, CONTINENTAL MARGIN, WESTERN ATLANTIC, GEORGES BANK TO WESTERN FLORIDA, USA

AUSTIN B. WILLIAMS[1]

ABSTRACT

Twenty-six species of decapod crustaceans in 16 families and 1 species of euphausiid are reported from the outer continental shelf, submarine canyons, and nearby slope of the eastern and southeastern United States. Station data are given for all collections made with the aid of submersible and surface vessels. Bathymetric and geographic distributions are summarized for six species (*Lithodes maja*, *Munida forceps*, *M. longipes*, *Chacellus filiformis*, *Dissodactylus juvenilis*, *Euchirograpsus americanus*) whose ranges are extended. Comparative descriptive notes are given for other forms that have uncertain identities and need further study (*Alpheus* cf. *amblyonyx*, sp. near *Ligur*, *Munidopsis* cf. *transtridens*).

Records of decapod crustaceans from the outer continental shelf, submarine canyons, and nearby slope off the eastern United States have accumulated in my files to the point that it seems appropriate to publish them with notes on the samples taken in that habitat. Specimens were collected with the aid of deep and shallow water submersibles and surface vessels operated cooperatively by the Lamont-Doherty Geological Laboratory, Columbia University, Palisades, NY, with sponsors listed hereinafter, and between Rutgers University, Center for Coastal and Environmental Studies, and Department of Horticulture and Forestry, New Brunswick, NJ; the Northeast Fisheries Center, National Marine Fisheries Service (NMFS), NOAA, Woods Hole, MA; and the Southeast Fisheries Center Laboratories, NMFS, NOAA, at Panama City, FL, and Pascagoula, MS (Able et al. 1982, 1987; Grimes et al. 1980a, 1986; and Lamont-Doherty records). Vessels (see Table 1) and their sponsoring institutions were DSRV *Alvin*, Woods Hole Oceanographic Institution, Woods Hole, MA; RV *JSL I* and *JSL II*, Harbor Branch Oceanographic Institution, Inc., Fort Pierce, FL; RV *Cape Henlopen*, University of Delaware, Lewes, DE; RV *Eastward*, Duke University, Beaufort, NC; RV *Endeavor*, University of Rhode Island, Kingston, RI; RV *Gyre*, Texas A&M University, Galveston, TX. The specimens have been deposited in the crustacean collection of the United States National Museum of Natural History (USNM).

Bathymetric and geographic distributions of many decapod crustacean species from the North American continental shelf in the western Atlantic were reviewed by Squires (1965), Williams and Wigley (1977), Wenner (1982), and Williams (1984). Wenner and Boesch (1979) and Wenner and Windsor (1979) included a deeper dwelling component in their treatments of epibenthic decapods collected from the continental shelf and slope. Collections by workers from the contributing institutions listed above include 26 species of decapod crustaceans in 16 families, some unidentified fragments, and 1 species of euphausiid listed in Table 1. Named localities are listed from north to south (see Figures 1 and 2); successive visits are arranged chronologically, and species present in each collection are inventoried alphabetically.

Species whose reported bathymetric or geographic ranges are extended by presence in these collections are discussed below. Some of the forms have uncertain identities that may be clarified after more thorough study of samples from the outer shelf-upper slope environment.

SUPERFAMILY ALPHEOIDEA

Family Alpheidae

Alpheus cf. *amblyonyx* Chace 1972. Three lots of specimens key out to *A. amblyonyx* (see Chace 1972), but they differ in several respects from it.

[1]Systematics Laboratory, National Marine Fisheries Service, NOAA, U.S. National Museum of Natural History, Washington, DC 20560

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TABLE 1.—Records of decapod crustaceans from submarine canyons, outer listed from north to south, successive visits are arranged chronologically, and in footnote. * = Bathymetric or geographic range extension.

Locality	Depth (m)	Cruise/ station	Date
---------- Lamont-Doherty ----------			
Lydonia Canyon			
40°21′N, 67°41′W	700-790	Gyre	8 June 1982
40°22′N, 67°41′W	462	Alvin 1269	18 Sept. 1982
40°21.69′N, 67°39.97′W	906	Alvin 1270	19 Sept. 1982
Oceanographer Canyon			
40°23.7′N, 68°07.8′W	415-680	Eastward 35982	15 May 1979
40°16.3′N, 68°07.2′W	660-1,424	Eastward 35991	19 May 1979
Slope Area III between Hydrographer and Veatch Canyons			
39°50′N, 69°25′W	500-2,000	Endeavor	21 Oct. 1981
Slope Area II between Toms and Meys Canyons			
39°13.05′N, 72°30.93′W	174	JSL I 1081	1 Aug. 1981
39°12.64′N, 72°30.87′W	200	JSL I 1081	1 Aug. 1981
39°11.06′N, 72°33.66′W	219	JSL I 1082	1 Aug. 1981
Hendrickson Canyon			
39°03.52′N, 72°28.45′W	1,420-1,425	Alvin 1118	19 July 1981
Baltimore Canyon			
38°09.6′N, 73°49.2′W	155-160	Eastward 35940	2 May 1979
38°07.9′N, 73°48.8′W	185-190	Eastward 35938	2 May 1979
38°08.5′N, 73°49.9′W	280-570	Eastward 35944	2 May 1979
38°09.6′N, 73°49.2′W	155-160	Eastward 35940	2 May 1979
38°08.7′N, 73°49.3′W	148-174	Eastward 35939	2 May 1979
38°11.7′N, 73°52.8′W	150-245	Eastward 35942	2 May 1979
38°03.6′N, 73°46.2′W	910-925	Eastward 35946	3 May 1979
38°07.6′N, 73°46.8′W	152-163	Eastward 35947	3 May 1979
38°06′N, 73°50′W	200-800	Eastward 35979	7 May 1979
38°04.93′N, 73°47.79′W	1,024	Alvin 1109	11 July 1979
38°08′N, 73°50.7′W	600-700	B10-1	28 May 1981
34°04′N, 73°46′W	1,000-1,200	Cape Henlopen CM02	13 June 1981
38°09′N, 73°51′W	171-381	JSL I 1083	2 Aug. 1981
38°09.99′N, 73°51.86′W	381	JSL I 1083	2 Aug. 1981
38°11′N, 73°51′W	165	JSL I 1088	4 Aug. 1981
38°11′N, 73°51′W	165-244	JSL I 1088	4 Aug. 1981
38°10.1′N, 73°52.2′W	225	JSL I 1084	4 Aug. 1981

continental shelf and upper slope off the eastern United States. Named localities are species inventoried in each collection are listed alphabetically. Family abbreviations

Species	*N*, Sex	Notes, family[1]
	---------- Lamont-Doherty ----------	
Munida valida Smith	1♂	Dredge, Ga
Pagurus politus (Smith)	1♂	Pag
**Munidopsis* cf. *transtridens* Pequegnat and Pequegnat	1♂	Ga
Pandalus propinquus G. O. Sars	1♀	Pan
Panadalus propinquus	1♂, 3♀	Day dredge, Pan
Metacrangon jacqueti agassizii (Smith)	1♂	Dredge, Cr
Nematocarcinus ensifer (Smith)	1 spec.	Camera, N
Euprognatha rastellifera Stimpson	1♀ ovig.	M
**Euchirograpsus americanus*	1♀	Gr
Eumunida picta Smith	1♀	Ch
Munida iris iris A. Milne Edwards	1♂ (parasitized)	Ga
**Munidopsis* cf. *transtridens*	1♂	Ga
Cancer borealis Stimpson	1 juv.	Can
**Euchirograpsus americanus* A. Milne Edwards	1♂, 3♀	Gr
Euprognatha rastellifera	1♂	Day dredge, M
Cancer borealis	1♀	Day dredge, Ca
Euprognatha rastellifera	1♂	Day dredge, M
**Munida longipes* A. Milne Edwards	1♂, 2♀ ovig.	Day dredge, Ga
Pagurus politus (Smith)	1♀	Day dredge, Pa
**Chacellus filiformis* Guinot	1♂	Day dredge, Go
Euprognatha rastellifera	1♂	Day dredge, M
Munida iris iris	3♂, 3♀	Day dredge, Ga
Plesionika edwardsii (Brandt)	1♀ ovig.	Day dredge, Pan
Cancer borealis	2 juv.	Day dredge, Ca
Cancer irroratus Say	1♂	Day dredge, Ca
Euprognatha rastellifera	1♂	Day dredge, M
Cancer borealis	1♂	Day dredge, Ca
Sergestes arcticus	1♀	Day dredge, S
Collodes robustus Smith	1♀ ovig.	Day dredge, M
Eumunida picta	4 juv., 1♂, 5♀	Camera sled, Ch
Lebbeus polaris (Sabine)	1♀	Camera sled, H
**Munidopsis* cf. *transtridens*	1♂	Airplane wreck, Ga
Sergestes arcticus Kröyer, euphausiid and copepods	9♀	Bongo net, S
Sergestes arcticus	1♀	Bongo net, S
Bathynectes longispina Stimpson	1♂	Po
**Lithodes maja* (Linnaeus)	1♀	L
Cancer irroratus	1♂	Ca
Munida iris iris	1♂	Ga
Munida iris iris	1♂	Ga
Pagurus politus	1♂	Pag

TABLE 1.—*Continued.*

Locality	Depth (m)	Cruise/ station	Date
38°09.51′N, 73°51.25′W	338	JSL I 1089	5 Aug. 1981
38°11′N, 73°51′W	402	JSL I 1090	5 Aug. 1981
38°02′N, 73°45′W	200-1,400	Gyre	26 May 1982
Norfolk Canyon			
37°03′N, 74°37′W	215	JSL I 1093	7 Aug. 1981
---------- Rutgers ----------			
Lydonia Canyon			
40°27.25′N, 67°42.30′W	160-178	JSL I 1070	23 July 1981
Veatch Canyon			
40°03′20″N, 69°45′23″W	124-126	JSL I 1074	25 July 1981
40°03′00″N, 69°45′25″W	123-128	JSL I 1075	26 July 1981
39°59′51″N, 69°35′00″W	213-244	JSL I 1076	26 July 1981
40°00.91′N, 70°50.79′W 40°01.29′N, 70°50.63′W	243-304	JSL II 901	29 July 1984
40°03.24′N, 71°05.01′W	193-209	JSL II 902	29 July 1984
40°02.96′N, 70°20.84′W	181-195	JSL II 909	2 Aug. 1984
40°12.73′N, 70°19.77′W	103-104	JSL II 910	2 Aug. 1984
40°12.51′N, 70°20.22′W	103-104	JSL II 910	2 Aug. 1984
40°02.79′N, 70°11.95′W	183-337	JSL II 911	3 Aug. 1984
40°03.23′N, 70°12.01′W	213-327	JSL II 912	3 Aug. 1984
Off eastern Florida			
28°43′N, 80°02′W	137	JSL I 1565	1 Oct. 1984
28°42.5′N, 80°02.8′W	98-114	JSL I 1566	2 Oct. 1984
Off western Florida			
27°51.2′N, 84°53.7′W	250-260	JSL I 1673	24 Sept. 1985
27°56.2′N, 84°43.9′W	167-175	JSL I 1676	26 Sept. 1985

[1]A, Alpheidae; Cal, Calappidae; Can, Cancridae; Ch, Chirostylidae; Cr, Crangonidae; Ga, M, Majidae; N, Nematocarcinidae; Pag, Paguridae; Pan, Pandalidae; Pi, Pinnotheridae; Po,

Species	*N*, Sex	Notes, family[1]
Rochinia crassa A. Milne Edwards	1♂	M
Pandalus propinquus	2♀	Pan
Sergestes arcticus	3♂	Camera, S
Bathynectes longispina	1 juv.	Po
---------- Rutgers ----------		
**Munida forceps* A. Milne Edwards	1♂	Bot. t. 11.2°C, Ga
Munida iris iris	1♂, 4♀ ovig.	Bot. t. 11.4°C, Ga
Pagurus politus	1♂	Bot. t. 11.4°C, Pag
Acanthocarpus alexandri Stimpson	2♀	Bot. t. 11.5°C, Ca
**Chacellus filiformis*	3♂ (1 juv.)	Bot. t. 11.2°C, Go
	4♀ (1 juv., 3 ovig.)	Bot. t. 12.2°C, Ga
**Munida forceps*	1♂, 1♀ ovig.	Bot. t. 12.2°C, Ga
Munida iris iris	1♂	
**Alpheus* cf. *amblyonyx* Chace	1♂	H
**Alpheus* cf. *amblyonyx*	1 juv.	H
Munida iris iris	1♂	Ga
**Munida forceps*	1♂	Ga
*Goneplacid? crab		Go
**Chacellus filiformis*	1♂,1♀	Go
**Munida forceps*	2♂	Ga
**Munida forceps*	1♂	Ga
Meganyctiphanes norvegica (M. Sars)	1	E
**Munida forceps*	1 juv., 1♀ ovig.	Ga
**Chacellus filiformis*?	Frag. of chela	Go
Meganyctiphanes novegica	45	E
Meganyctiphanes novegica	2	E
Meganyctiphanes novegica	8	E
Alpheus cf. amblyonyx	2♂, 1♀, 1 juv.	Tilefish burrow, A
Munida forceps	2♀	Tilefish burrow, Ga
Crab (xanthid or goneplacid frags.)	1	Tilefish burrow, Ga
**Alpheus* cf. *amblyonx*	1♀	Tilefish burrow, Ga 12.1°C, A
Munida forceps	1	Tilefish burrow, Ga
*Near *Ligur* Sarato	2♂, 1♀	Tilefish burrow, Hi
**Munida forceps*	1♂, 2♀ ovig. 1 juv.	Tilefish burrow, Ga
**Dissodactylus juvenilis* Bouvier	1♀ ovig.	With *Clypeaster ravenellii* A. Agassiz, 13.8°C, Pi

Galatheidae; Go, Goneplacidae; Gr, Grapsidae; E, Euphausiidae; H, Hippolytidae; L, Lithodidae; Portunidae; S, Sergestidae.

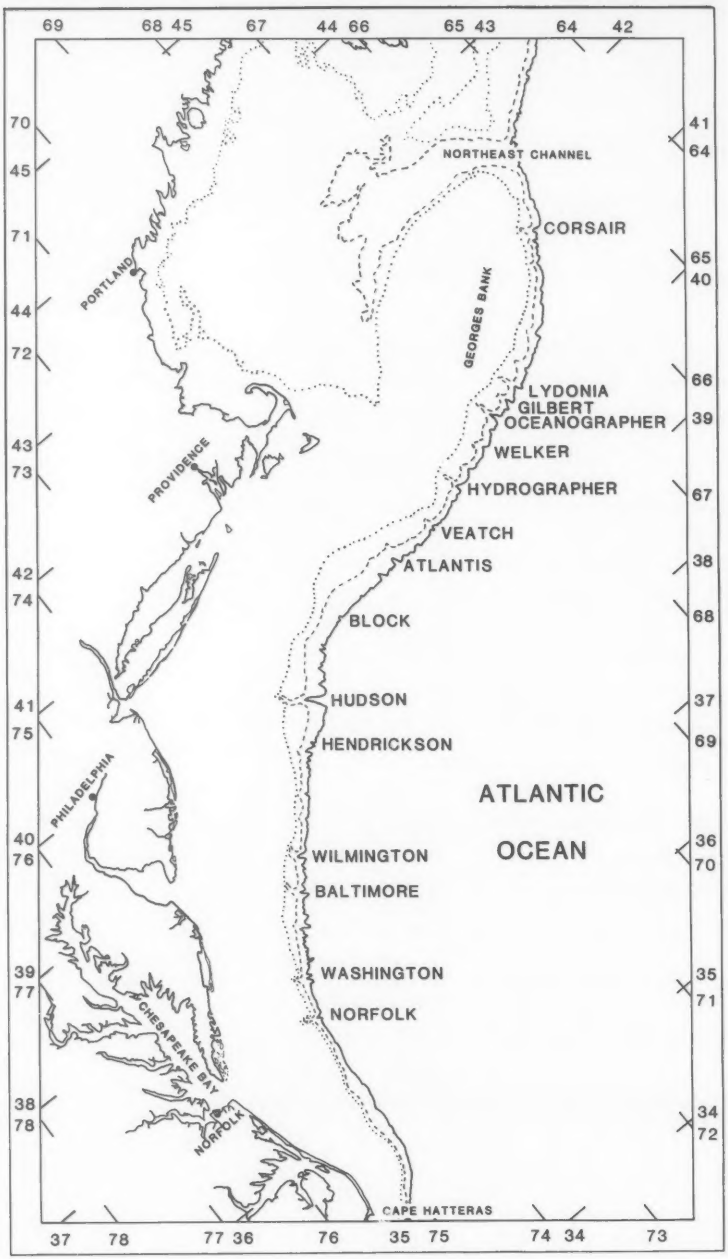

FIGURE 1.—East coast of United States showing continental shelf, slope and submarine canyon areas from which species listed in Table 1 were collected. Base map adapted from Uchupi (1965) and Veatch and Smith (1939). Contours in m: dotted = 100, dashed = 200, solid = 1,000.

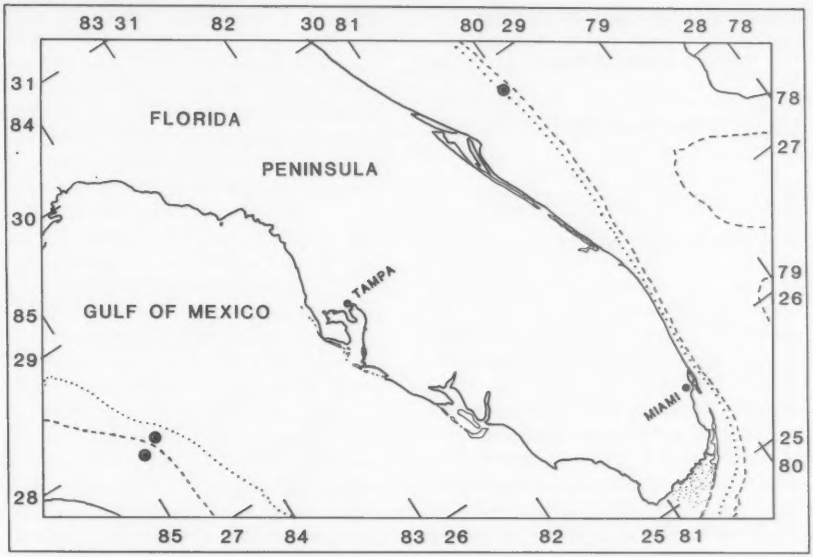

FIGURE 2.—Florida peninsula including continental platform showing slope localities from which species listed in Table 1 were collected. Base map adapted from Uchupi (1965). Contours in m: dotted = 100, dashed = 200, solid = 1,000.

Some of the more obvious differences for the Veatch Canyon material are: Rostrum relatively shorter in relation to basal antennal article. Dorsal spines of telson more distally positioned, anterior pair at about midlength of telson but subject to some variation. Antennal scale with distal spine exceeding antennular peduncle. Major chela of mature male missing, but juvenile with fingers bent mesad; dactyl moderately arched in profile and greatly overreaching fixed finger, somewhat twisted, compressed proximally and dorsally producing thin dorsal margin, external surface somewhat concave, occlusive surface lacking plunger but broadened and strongly calcified distally, fitted to obliquely flattened occlusive surface of fixed finger lacking socket but provided with small stout tooth on mesial surface; palm with obsolescent dorsal and ventral notches.

In the Florida material, the differences are: Chela relatively stout, fingers stout and thick, dactyl opening and closing in oblique plane, tip rounded, bearing short plunger fitting into shallow socket on occlusive surface of fixed finger, latter with 2 short spines on mesial surface; palm with shallow notch on dorsal margin and slight offset on ventral margin, outer surface smooth but base of dactyl flanked by distodorsal groove and longer mesial groove. Second pleopod of male with appendix masculina exceeding appendix interna. Uropodal exopod with lateral margin ending in single sharp tooth and rather long, uncolored movable spine; endopod lacking distal spines but bearing subterminal tuft of setae on dorsal surface.

Alpheus amblyonyx is distributed from Quintana Roo (type locality, Bahía de la Ascensión), Yucatan Peninsula, Mexico, to Puerto Rico, Saint Thomas and Dominica; sublittoral (Chace 1972).

Family Hippolytidae

Three small shrimps, two males and one female from *JSL* 1673 in the Gulf of Mexico off Florida, represent an undescribed species resembling members of the genus *Ligur* Sarato, 1885 from the western Mediterranean and Indo-Pacific region (see Holthuis 1947, 1955). The specimens were associated with burrow systems of the blueline tilefish, *Caulolatilus microps* Goode and Bean.

SUPERFAMILY PAGUROIDEA

Family Lithodidae

Lithodes maja (Linnaeus 1758). Southern limit extended from Sandy Hook, NJ (see Williams 1984) to Baltimore Canyon.

SUPERFAMILY GALATHEOIDEA

Family Galatheidae

Munida forceps A. Milne Edwards 1880. Geographic range extended from south of Norfolk Canyon, 36°43.2′N, 74°38.0′W, 252 m (Wenner 1952), to Veatch and Lydonia Canyons off southern New England, 103-337 m.

The distinctive color pattern of this species was described on 14 October 1981 from specimens preserved in formalin 25 July 1981. Carapace (Fig. 3), salmon color with lavender submesial spots on gastric region and interrupted U-shaped bands of same color in nested series on mesogastric region, posterior to cephalic groove, and arching across posterior and posterolateral parts. Oblique red lines on lateral wall of carapace below suture, most prominent band along anterior edge, continued dorsally anterior to antennal peduncle and ending on lateral side of supraocular spine. Median band of same intensity on epistome and labium. Paler oblique lateral band on basal antennular article. Some flecks of red on merus of chelipeds and cross banding on fingers of some individuals.

Munida longipes A. Milne Edwards 1880. Northern limit extended from off Cape Lookout, NC (Williams 1984) to Baltimore Canyon.

Munidopsis cf. *transtridens* Pequegnat and Pequegnat 1971. *Munidopsis transtridens* is known only from the holotype female taken in the southeastern Gulf of Mexico at 1,280 m. The specimens reported here from Baltimore, Hendrickson, and Lydonia Canyons off New Jersey and southern New England, 906-1,425 m, are all males. They resemble *M. transtridens* but differ from it in rostral characters (both longer and shorter, variably narrower or broader, in degree of lateral convexity) and in having chelae strikingly larger than the slender ones of the holotype. Although these differences may be attributable to sexual dimorphism, provisional identification seems best until more material is available for study.

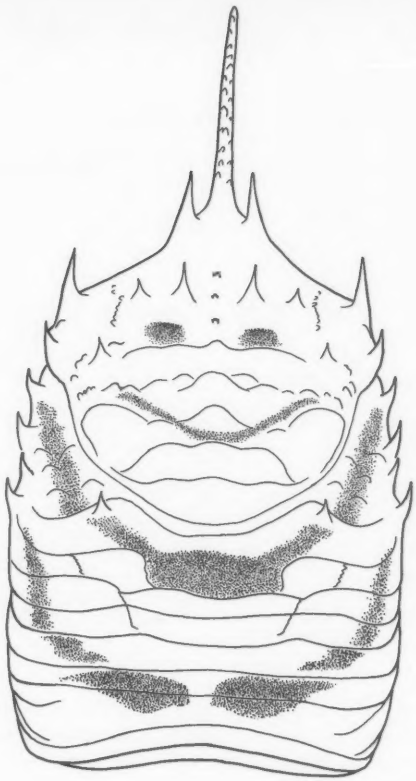

FIGURE 3.—*Munida forceps*, male. Dorsal view of carapace, diagrammatic representation of lavender bands on salmon ground color, carapace length 17.7 mm to base of supraocular spine.

SUPERFAMILY XANTHOIDEA

Family Goneplacidae

Chacellus filiformis Guinot 1969. Geographic range extended from the northern Gulf of Mexico east of the Mississippi River Delta and off the east coast of Florida, 328-400 m (Guinot 1969), to Baltimore and Lydonia Canyons, 160-244 m.

Goneplacid crabs were driven out of secondary burrows in walls of larger burrows constructed by tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, with rotenone. The poison did not kill the crabs but caused them to emerge from the burrow systems enough that they could be collected by

"slurp gun". These burrow systems in Pleistocene clay, referred to by Warme et al. (1978) and Cooper and Uzmann (1980) as "Pueblo Villages", shelter a number of invertebrate and vertebrate species (Able et al. 1982; Bowman 1986; Grimes et al. 1980a, 1980b, 1986). Goneplacids are rare in collections made from surface vessels probably because trawls or grabs cannot efficiently sample the burrow systems in which these crabs have been observed. Galatheids from shallower burrows are more open to capture by conventional means (Churchill B. Grimes[2]).

To the brief color description quoted from Chace by Guinot (1969), the following can be added from notes made 14 October 1981 on mature males, females, and juveniles that were preserved in formalin 25 July 1981, and personal communication from Churchill Grimes (fn. 2). Carapace dorsally spotted with red on off-white background. Same type of spots on pterygostomian, subocular, epistomial, and subbranchial areas, on external maxillipeds, and on merus, carpus, and propodus of chelipeds (dorsally, laterally, and mesially). Spots tending to coalesce along front of carapace and on chelae. Red color more diffuse on dorsal or exposed surfaces of walking legs, becoming more distinct and intense with increasing size. Fingers of chelae black. Dactyls of walking legs white except for darkened tips, but setae pinkish. There is some variation in pattern on individual crabs.

There is variation also in the length of the male first pleopod, both in the USNM series of specimens studied by Guinot (1969) and in the new material reported here. In some specimens of the latter, this appendage exceeds or at least reaches the distal edge of the telson, whereas it is shorter in specimens previously reported from localities further south. In the latter, the third abdominal segment is more angled laterally than in specimens from the north. Thus, there seem to be some differences between the northern and southern populations.

SUPERFAMILY GRAPSIDOIDEA

Family Grapsidae

Euchirograpsus americanus A. Milne Edwards 1880. Geographic range extended north from off Oregon Inlet, NC (Williams 1984) to Oceanographer Canyon at the edge of Georges Bank and nearby continental slope at 155-200 m.

SUPERFAMILY PINNOTHEROIDEA

Family Pinnotheridae

Dissodactylus juvenilis Bouvier 1917. The ovigerous female from the Gulf of Mexico off western Florida, though similar in general features to *D. juvenilis*, is very large for that species. In a recent review of the genus *Dissodactylus*, Griffith (1987) reported *D. juvenilis* from north of Yucatan and the Mississippi Delta. Members of the genus are found in association with clypeastroid echinoids (Schmitt et al. 1973), as was this specimen in a sample that included *Clypeaster ravenellii* A. Agassizi.

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AGE AND GROWTH OF LARVAL GULF MENHADEN, *BREVOORTIA PATRONUS*, IN THE NORTHERN GULF OF MEXICO

STANLEY M. WARLEN[1]

ABSTRACT

Experiments on laboratory-spawned and -reared larval gulf menhaden, *Brevoortia patronus*, showed that they formed one otolith growth increment p_r day and that the increments could be used to estimate their age. Wild larvae from collections in the northern Gulf of Mexico along three transects (Cape San Blas, Florida; Southwest Pass, Louisiana; and Galveston, Texas) were aged. Gompertz growth equations were used to describe the relationship between age and standard length for larvae collected at various locations, and in different seasons and years. MANOVA tests and subsequent pairwise tests were used to test for differences among these growth curves. For the most extensive data set (Southwest Pass, Louisiana), there were significant differences in growth between early season (December) and late season (February) larvae. Early season larvae grew faster than late season larvae. Growth of larvae also differed among December collections and among February collections. The growth model for the pooled data for all wild larvae predicted that they grew from 2.4 mm SL at hatching to 20.4 mm SL at 62 days.

Gulf menhaden, *Brevoortia patronus*, is the most abundant commercial finfish in the Gulf of Mexico and, with 883,500 metric tons (t) landed in 1985 (U.S. National Marine Fisheries Service 1986); it constitutes the largest fishery in the United States. Some aspects of the oceanic early life history of this clupeid are known and are reviewed by Turner (1969), Christmas and Waller (1975), Lewis and Roithmayr (1981), Govoni et al. (1983), and Shaw et al. (1985a). However, virtually nothing is known about the age and growth of the larvae, much less how these parameters vary spatially and temporally. Daily growth increments on otoliths of larval fishes can be used as an indicator of their age, and once the use of this technique, first described by Pannella (1971), is validated for the larvae of an individual species, their ages can be estimated with confidence and growth rates can be determined. Intraspecific growth may be compared for larvae from different areas and seasons (Lough et al. 1982), and from this it may be possible to ascertain how biotic and abiotic environmental variables affect larval growth and survival. The objectives of this study are to 1) validate the periodicity of increment formation in otoliths of larval gulf menhaden, 2) estimate larval growth rates, 3) compare growth rates of larvae from different locations and times, 4) estimate spawning times, and 5) examine possible relationships between larval growth and surface water temperature. This work was part of a larger project designed to investigate the early life history of several economically important fishes and the marine planktonic food webs that support their growth and survival in the northern Gulf of Mexico.

METHODS

Spawning and Larval Rearing

Adult gulf menhaden were collected near Gulf Breeze, FL, and transported to the Beaufort Laboratory, Beaufort, NC (Hettler 1983). After a period of acclimation, adults were induced to spawn in the laboratory. The resultant larvae were used in experiments to validate the periodicity of increment formation on their otoliths and the age at first increment formation.

Beginning February 1983, several thousand newly spawned gulf menhaden eggs were transferred to a tank containing 90 L of filtered seawater. The static water in this tank, kept at 20.5° ± 0.5°C throughout the experiment, was continuously aerated and the salinity maintained at 31 ± 1‰. Photoperiod was 12 hours light:12 hours dark. A food concentration of 25 rotifers (*Brachionus plicatilis*) mL^{-1} was maintained. A green alga, *Nanochloris* sp., was added periodically as food for the rotifers and to aid in removing toxic metabolites. The otoliths of larvae sam-

[1]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

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pled at 10-, 17-, 24-, and 31-d posthatch were examined.

In January 1984 additional larvae were reared to compliment results of the earlier experiment. Smaller tanks with 60 larvae in 10 L of filtered water were used. Experimental conditions were the same as for the first experiment. The otoliths of larvae sampled at 7-, 14-, and 20-d posthatch were examined.

Larval Collections

Larval gulf menhaden were collected in the northern Gulf of Mexico during six cruises of the RV *Oregon II*. Sampling stations (Fig. 1) along transects LA (off Louisiana) and FL (off Florida) were occupied during 11–19 December 1979, 5–15 February 1980, and 2–12 December 1980 and along transects LA, FL, and TX (off Texas) during 9–24 February 1981, 2–13 December 1981, and 4–16 February 1982. Transect LA is near the Mississippi River outflow off Southwest Pass, LA; transect FL is southwest of Cape San Blas, FL; and transect TX is located off Galveston Bay, TX. Sampling stations were in water depths of 18, 91, and 183 m except off Texas where only the 18 and 91 m depths were sampled.

A multiple opening-closing net and environmental sensing system (MOCNESS) as described by Wiebe et al. (1976) were the primary sampling gear used to capture larvae. Additional samples were taken in oblique tows with a 60 cm bongo frame also fitted with 505 μm mesh nets. Samples were collected day and night and were preserved in 95% ethanol (final concentration ≈75%) within 5 minutes of collection. The ethanol was changed in all samples at least once after initial preservation to prevent dissolution of otoliths in fish from any samples that may have been inadequately preserved. Data from larvae collected at all stations within a transect were combined for that transect.

Estimating Age and Growth

All gulf menhaden larvae were measured to the nearest 0.1 mm standard length (SL). The largest otolith pair (sagittae) was teased from the surrounding tissue, cleaned in distilled water, and then placed on a glass microslide under a thin layer of Flo-Texx[2] mounting medium.

Otoliths were viewed with a compound microscope fitted with a television camera. Growth increments were counted from otolith images on a video monitor at magnifications of at least 400×. An increment appeared as a light, wide incremental band and a dark, narrow, discontinuous band (Tanaka et al. 1981). Increments were generally clearly discernable and easily counted (Fig. 2). Estimated age was the number of increments counted plus an empirically derived value for the

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

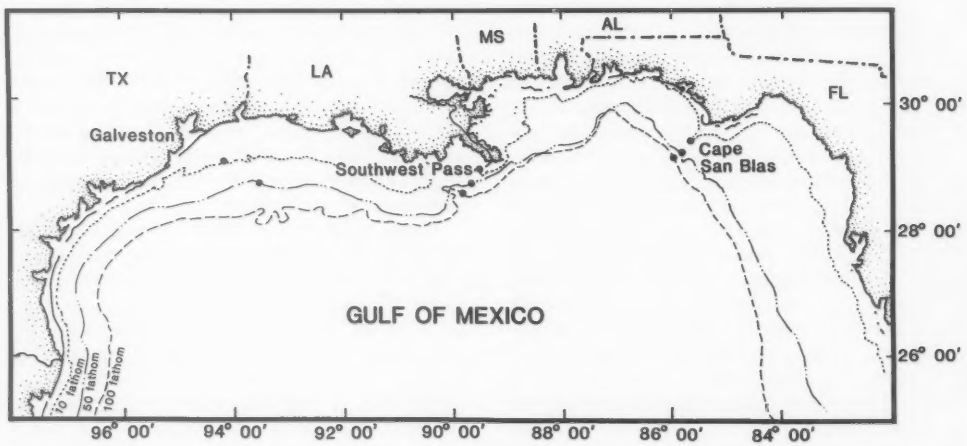

FIGURE 1.—Location of sampling sites from which larval gulf menhaden were collected during cruises of the RV *Oregon II* in December 1979–81 and February 1980–82.

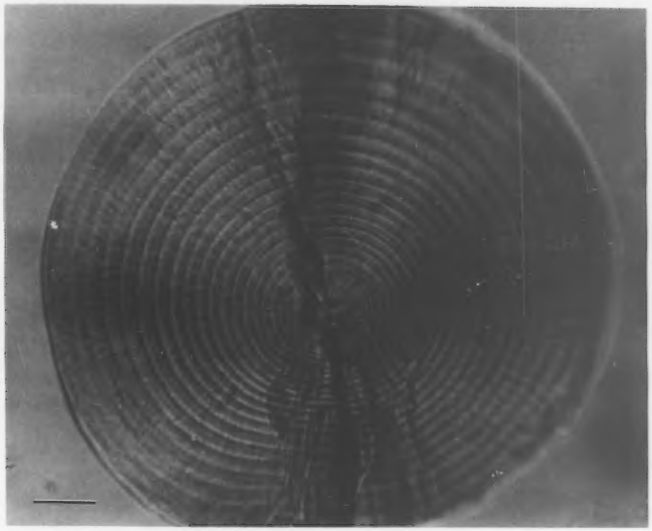

FIGURE 2.—Photomicrograph of a saggital otolith with 22 increments from a 17.4 mm SL field collected larval gulf menhaden. Scale bar represents 10 μm. Growth increments appear as pairs of wide incremental and narrow discontinuous bands.

number of days from spawning to first increment formation. Results of the laboratory experiments established the periodicity of otolith increment formation.

A spawning date was assigned each ageable larva by using the estimated age of the fish in days to back-calculate from the date of capture. It was assumed that there were no differences in either the age at initial increment deposition or the otolith increment deposition rate between locations and seasons and that the rate was not a function of temperature, food, or photoperiod.

Average growth of larvae was described by the Laird version (Laird et al. 1965) of the Gompertz growth equation (Zweifel and Lasker 1976) fitted to estimated age and size at time of capture for fish from all cruises and transects. To stabilize the variance of length over the observed age interval, length data were log-transformed and model parameters were estimated from the log-transformed version of the growth equation. The model was fit to data for each transect within each cruise and for pooled data from all cruises.

Potential differences in the overall growth curves among years and between seasons for larvae caught off Louisiana and between years (1981 and 1982) for larvae caught off Louisiana and Texas were examined by treating the parameters of the Gompertz equation as dependent variables in two-way multivariate analysis of variance (MANOVA) designs. A one-way MANOVA design was used to test for differences among transects (LA, FL, TX) within one season (February 1982). Following significant MANOVA results, prespecified pairwise Hotelling's T^2 test comparisons (Bernard 1981, as modified by Hoenig and Hanumara 1983) were made using the Bonferroni procedure (Harris 1975) to provide conservative tests of statistical significance. Bonferroni critical values for these individual tests were equal to the overall error rate (significance level = 0.05) divided by the number of possible comparisons in the particular MANOVA design. The emphasis in the comparisons was to look for overall differences in the growth of larvae using these statistics as a guide and not to look for differences in individual parameters of the growth models.

Hotelling's T^2 test and MANOVA both require that the data fit a multivariate normal distribution and that the variance-covariance matrices of the populations are not different (Harris 1975). These assumptions are difficult to test and are almost certainly not valid for real data sets (par-

ticularly field data), but they may be nearly valid for many sets of data (Harris 1975). No direct test of normality in a trivariate, joint probability distribution is available (Bernard 1981), but bias arising from nonnormal, multivariate, joint distributions is minimized with large sample sizes (Bernard 1981). While methods are available to test the hypothesis of equal variance-covariance matrices (e.g., Box's modification of Bartlett's test), these methods are very sensitive and even minor differences between group dispersions will likely be discovered (Pimentel 1979). In any event, the use of MANOVA in this paper relies on variance-covariance matrices estimated from nonlinear regressions, and these are not amenable to testing. However, both MANOVA and Hotelling's tests are extremely robust even under violation of the assumptions of homoscedasticity and multivariate normality (Harris 1975).

RESULTS

Increment Formation

The age of gulf menhaden at formation of the first otolith growth increment was estimated from laboratory-reared larvae. The intercept (2.6 days) of the regression of the number of growth increments on known posthatch age of 36 larval gulf menhaden (Fig. 3) was used to estimate posthatch age at formation of the first increment. This value was added to the time from spawning to hatching which at 20°C is 2 days (Powell[3]). This sum (4.6 days) is the estimated time from spawning to formation of the first increment. Hence, it was necessary to add 5 days to each increment count to estimate the age of larval gulf menhaden from spawning.

The periodicity of increment formation was ascertained from the regression of the number of growth increments on the known age (Fig. 3). The slope did not differ significantly (t-test, $P < 0.05$) from 1.0, and thus, on the average, one otolith growth increment was formed per day in laboratory-reared larvae up to 31 days after hatching. Results of a second experiment (Table 1) confirmed this periodicity. The age of gulf menhaden larvae estimated from otolith increment counts (+5) closely approximated the known ages of 51 laboratory-reared larvae. Mean estimated age of larvae differed by <1 day from the known

[3]A. B. Powell, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722, pers. commun. February 1986.

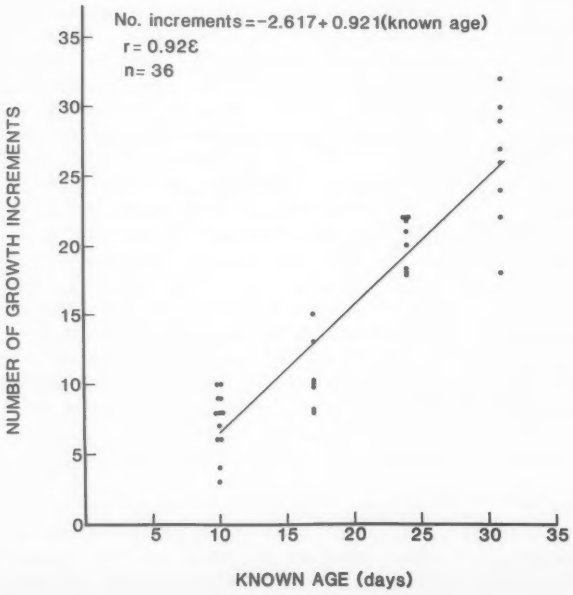

FIGURE 3.—Regression of the number of growth increments on the known posthatch age of 36 laboratory-reared gulf menhaden. Standard error of the slope is 0.108.

TABLE 1.—Standard length (mm) and estimated age (number of otolith growth increments +5) of laboratory-reared larval gulf menhaden. Values in parentheses are 95% interval estimates.

Known age (days)	Number of fish	Mean estimated age	Mean SL
7	13	7.8 (±0.38)	4.7 (±0.28)
14	16	13.2 (±1.14)	6.4 (±0.38)
20	22	19.3 (±0.77)	8.0 (±0.42)

ages and the 95% confidence intervals included the known age in each of the three groups. Some of the variation in the number of growth increments observed in known age larvae (Fig. 3, Table 1) may have been due to 1) poor growing conditions during rearing that could have resulted in reduced growth in underfed larvae, 2) variation in the inception of increment formation as has been observed in other species (Laroche et al. 1983; Fives et al. 1986), and 3) faintness of growth increments in some larvae. In contrast, increments on otoliths of field collected larvae (Fig. 2) were usually very regular and distinct and were more easily observed than those on otoliths of laboratory-reared larvae. I assumed that the growth increment deposition rate was also daily in wild larvae examined in this study.

Age and Growth of Larvae

Average growth of larval gulf menhaden during their first two months of life was described by the Gompertz growth model for pooled length at age data for 2,003 fish representing collections from all six RV *Oregon II* cruises (Table 2, Fig. 4). Larvae ranged in age from 5 to 62 days ($\bar{x}$=24.4 days) and in SL from 3.4 to 28.0 mm ($\bar{x}$=12.6 mm). In the log-transformed model, age accounted for 82% of the variation in length. Gulf menhaden were predicted to have grown from 2.4 mm SL at hatching to 20.4 mm at age 62 days. The size at hatching estimated from the Gompertz equation was only slightly less than the hatching size, 2.6–3.0 mm SL, observed in the laboratory (Hettler 1984). Age-specific growth rates declined from ≃7%/day at age 10 days to <0.4%/day at age 60 days. Maximum absolute growth rate occurred when gulf menhaden larvae were 7.9 mm SL and 13 days old.

The asymptotic length of larvae (21.5 mm SL), determined from the variables of the growth equation, is approximately the size when larvae begin to transform into juveniles. This transformation, described by Lewis et al. (1972) for the closely related Atlantic menhaden, *B. tyrannus*, apparently ends when the fish reach 28–30 mm SL (Suttkus 1956).

In all instances except one transect (TX December 1981, where there was no convergence in the parameter values in the computer fitting procedure and the model would not fit the data), the Gompertz growth model could be used to describe the growth of gulf menhaden larvae from each cruise and transect (Figs. 5-7, Table 2). The growth model for the FL December 1980 larvae approximates an exponential form because of the exceptionally low value for α. This may be due to the preponderance of small, young larvae.

GROWTH COMPARISONS

Louisiana - Seasons and Years

There were statistically significant differences (MANOVA, $P < 0.001$) in the growth curves for larvae caught off Louisiana for two seasons (December, February) and three years (1979-80, 1980-81, 1981-82). To determine if differences existed between seasons in each year and among any two years within each season, I selected 9 of the possible 15 pairwise comparisons for testing. The Bonferroni critical value in these tests was 0.0033 (0.05/15). The inability to fit a Gompertz growth model to the TX December 1981 data precluded a comparison with the larvae collected off Texas in February 1982.

Pairwise comparisons for within years data for Louisiana larvae showed significant differences ($P < 0.003$) in growth curves between early season (December) and late season (February) for each year. Faster growth of early season larvae is evident if the respective curves (Figs. 5; 6a, c; 7a, c) are compared. For any age, the predicted size is greater for early season than for late season larvae. Only for the third year did the length at age 40+ days of February-caught larvae exceed that for December-caught larvae.

In similar comparisons for larvae caught off Louisiana in December of all three years, there were significant differences ($P < 0.003$) in the growth curves (Figs. 5a, 6a, 7a) for any two years. As judged by the predicted size at any age, larvae appeared to grow faster in 1979 than in either 1980 or 1981. While the curves for the 1980 and 1981 larvae overlapped, larvae from 1980 were larger at 30+ days than were the 1981 larvae. Significant differences were also found among the curves (Figs. 5b, 6c, 7c) for larvae caught in

TABLE 2.—Estimates of Gompertz growth model parameters and mean age (days) and mean SL (mm) for larval gulf menhaden collected in the northern Gulf of Mexico during the winters 1979-80, 1980-81, and 1981-82. R^2 is the coefficient of determination for the respective models.

Date	Transect[1]	Number fish aged	R^2	Growth model parameters[2] $L_{(0)}$	$A_{(0)}$	α	Mean estimated age (d)	Mean SL (mm)
Winter 1979-80								
Dec. 1979	LA	42	0.863	2.768 (1.270)	0.1701 (0.0711)	0.0809 (0.0190)	28.1	17.4
Feb. 1980	LA	324	0.954	2.131 (0.138)	0.1592 (0.0105)	0.0710 (0.0031)	30.2	12.7
Winter 1980-81								
Dec. 1980	LA	191	0.931	2.888 (0.188)	0.1125 (0.0097)	0.0496 (0.0044)	22.0	11.8
Dec. 1980	FL	80	0.701	3.418 (0.994)	0.0561 (0.0370)	0.0001 (0.0407)	14.9	7.9
Feb. 1981	LA	338	0.849	2.702 (0.231)	0.1159 (0.0120)	0.0577 (0.0049)	24.6	11.7
Feb. 1981	TX	223	0.526	5.839 (0.579)	0.0305 (0.0088)	0.0125 (0.0110)	21.5	10.3
Winter 1981-82								
Dec. 1981	LA	370	0.921	0.384 (0.076)	0.4780 (0.0433)	0.1240 (0.0054)	21.7	13.3
Dec. 1981	TX	114	—	—[3]	—[3]	—[3]	25.4	11.9
Feb. 1982	LA	191	0.736	0.807 (0.337)	0.2729 (0.6093)	0.0851 (0.0090)	31.2	15.5
Feb. 1982	FL	88	0.624	2.278 (0.824)	0.1067 (0.0454)	0.0394 (0.0205)	17.6	8.9
Feb. 1982	TX	42	0.946	1.798 (0.392)	0.1276 (0.0340)	0.0500 (0.0142)	22.5	10.0
All years								
All data pooled		2,003	0.822	2.355 (0.098)	0.1345 (0.0059)	0.0608 (0.0020)	24.4	12.6

[1]LA=Mississippi River Delta (Southwest Pass Louisiana); FL=Cape San Blas, FL; TX=Galveston, TX.
[2]$L_{(0)}$=length at hatching, $A_{(0)}$=specific growth rate at hatching, α=exponential decline in $A_{(0)}$. Values in parentheses are estimated standard errors from the nonlinear regressions.
[3]Gompertz growth model did not fit the data.

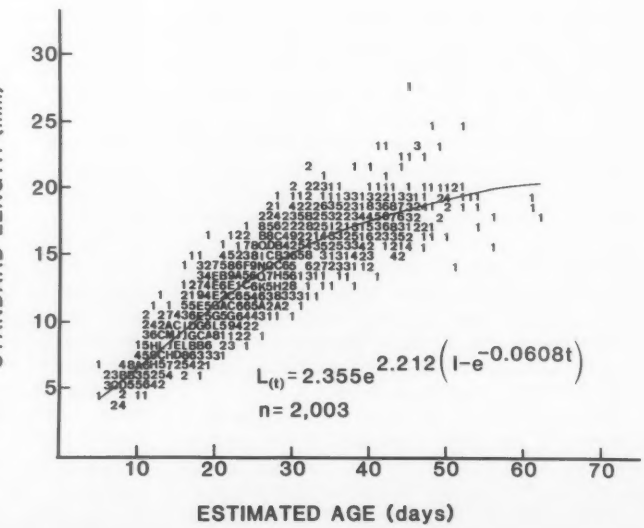

FIGURE 4.—Growth of gulf menhaden larvae collected in the winters of 1979–80, 1980–81, and 1981–82 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the pooled data. Two through nine coincident data points are labelled with their numeral. Coincident points of 10 and above are labelled A, B, etc.

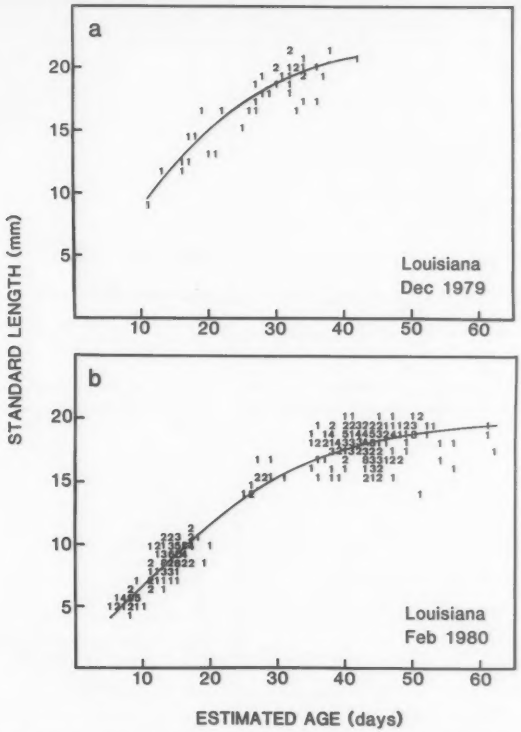

FIGURE 5.—Growth of larval gulf menhaden collected in the winter 1979–80 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the data. Coincident data points are labelled as in Figure 4.

February in three years. Larvae caught in 1980 grew faster than larvae caught in 1981 and larvae caught in 1982 up to 25 days, thereafter 1980 and 1982 had very similar size at age estimates.

Louisiana vs. Florida vs. Texas - February 1982

There were no significant differences (MANOVA, $P = 0.212$) among the growth curves for larvae caught in February 1982 off Louisiana, Texas, and Florida (Figs. 7c, d, e), and hence no pairwise comparisons were necessary.

Louisiana vs. Texas - February 1981–82

Statistically significant differences (MANOVA, $P < 0.002$) in larval growth were observed in the LA and TX transects from February 1981–82. Pairwise comparisons indicated significant differences ($P < 0.008$) in the growth of larvae collected off Texas in 1981 (Fig. 6d) and 1982 (Fig. 7e) and in growth between LA 1981 (Fig. 6c) and TX 1981 collections. The earlier pairwise comparisons had already shown a significant difference in growth of larvae from LA February 1981 and February 1982 collections (Fig. 7c), but none for growth of larvae caught in the LA February 1982 and TX February 1982 collections. Two other potential tests, between transects of different areas and different years, were not considered to be meaningful.

Larvae caught off Louisiana in February 1981 were larger at age 18+ days than were larvae caught off Texas in February 1981, and might be considered to be faster growing fish. There was a

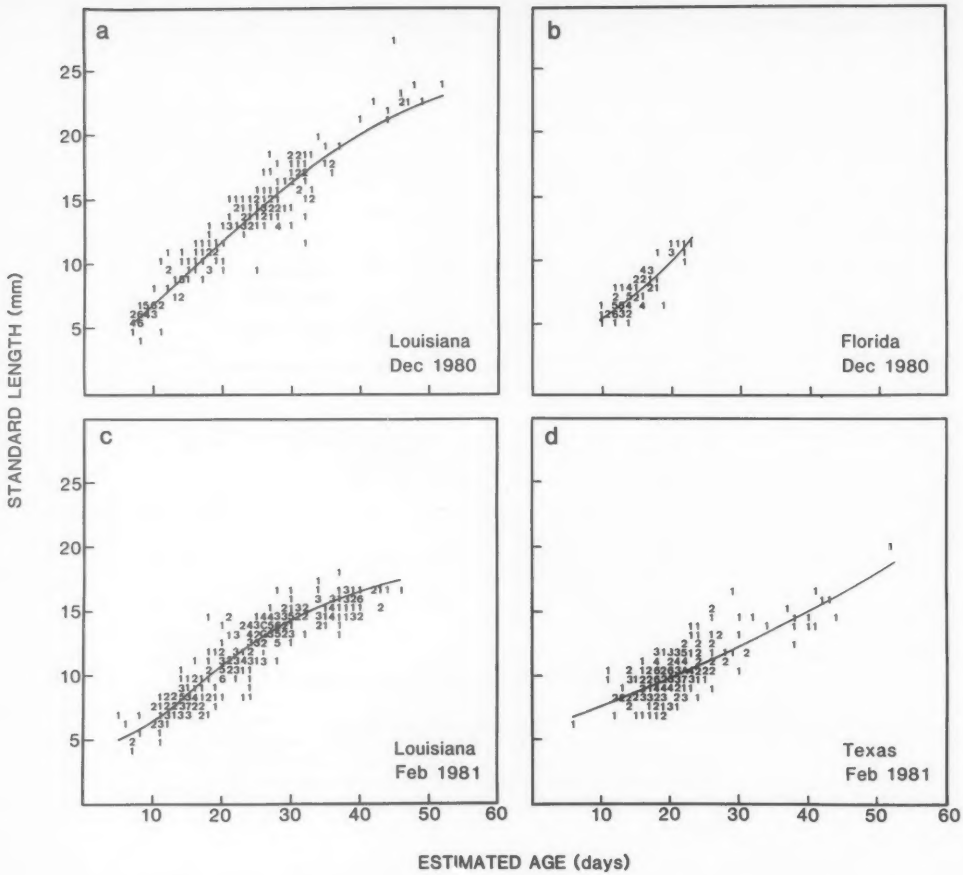

FIGURE 6.—Growth of larval gulf menhaden collected in the winter 1980–81 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the data. Coincident data points are labelled as in Figure 4.

statistical difference in growth of larvae caught off Texas in February 1981 and 1982, and it appears that the 1982 larvae grew at a faster rate. Conclusions from these statistical differences involving TX February 1981 larvae collections should be viewed with caution because of the relatively poor fit ($r^2 = 0.526$) of the model. Inadequacies, such as the lack of larvae <13 or >31 days old, in that data set probably resulted in the relatively poor parameter estimates (Table 2). Additional sampling would be necessary to further test the hypotheses of differences in growth between geographic areas in the northern Gulf of Mexico and between years for Texas larvae.

Estimated Spawning Times

Gulf menhaden larvae observed in this study were estimated to have been spawned from mid-October to mid-February (Fig. 8). The limited extent of seasonal sampling precluded estimation of the probable total range of the spawning season. Most larvae captured in December and February had been spawned in November and January respectively (Fig. 8). The considerable overlap in spawning times of larvae caught the same month in different years is a reflection of the similarity of sampling dates. The relatively narrow distribution of spawning dates for larvae caught off Flor-

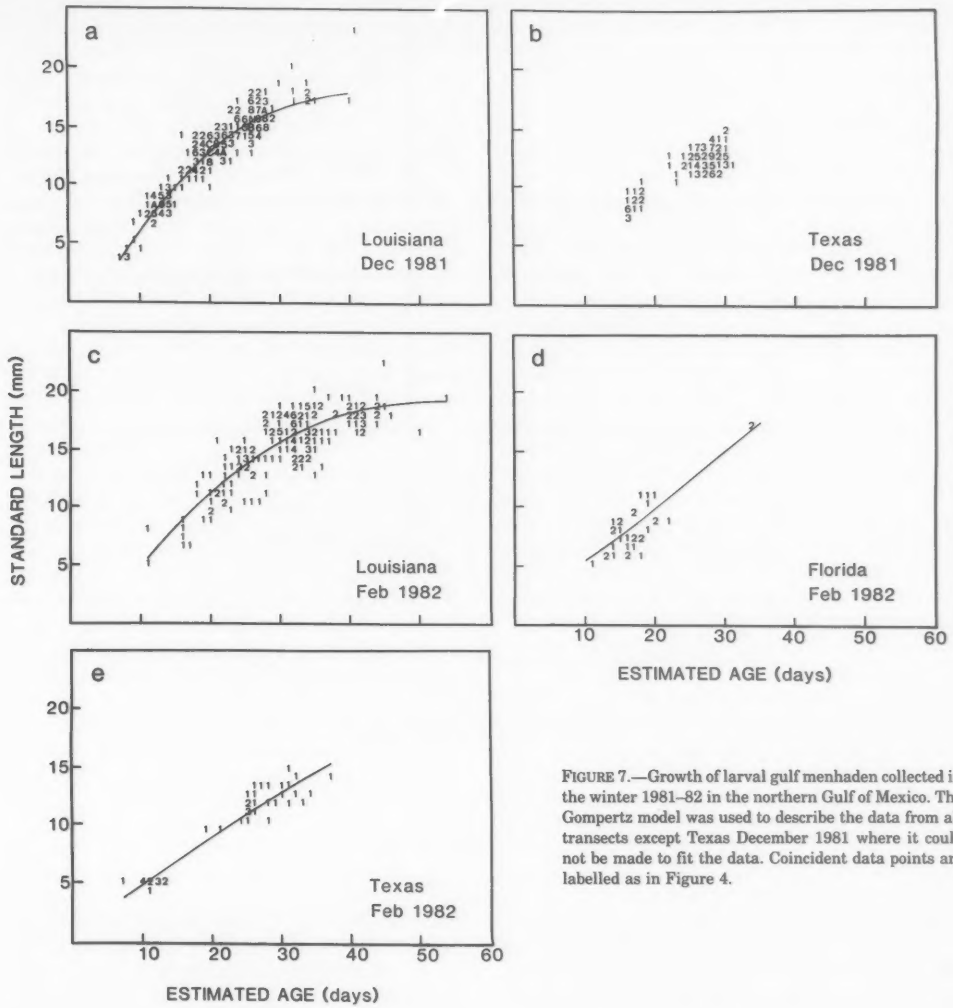

FIGURE 7.—Growth of larval gulf menhaden collected in the winter 1981–82 in the northern Gulf of Mexico. The Gompertz model was used to describe the data from all transects except Texas December 1981 where it could not be made to fit the data. Coincident data points are labelled as in Figure 4.

ida in both December 1980 (Fig. 6b) and in February 1982 (Fig. 7d), off Louisiana in February 1982 (Fig. 7c), and off Texas in February 1981 (Fig. 6d) represent larvae from fewer cohorts.

DISCUSSION

Laboratory observations indicate that larval gulf menhaden on the average form one growth increment per day on their otoliths and that counts of these increments can be used to estimate age. Otoliths of larval gulf menhaden are thin and round, and the increments are generally easily counted and consequently are ideally suited for ageing. The most closely spaced increments, those occurring near the focus, were at least 1.5 μm wide and were above the 0.2 μm resolution of the light microscope (Campana and Neilson 1985). First increment formation occurs about 5 days after spawning and probably coincides with first exogenous feeding. This is supported by Hettler (1984) who found that gulf menhaden eggs hatched at about day 1.7 at 19°-20°C. Four days after hatching larvae had functional

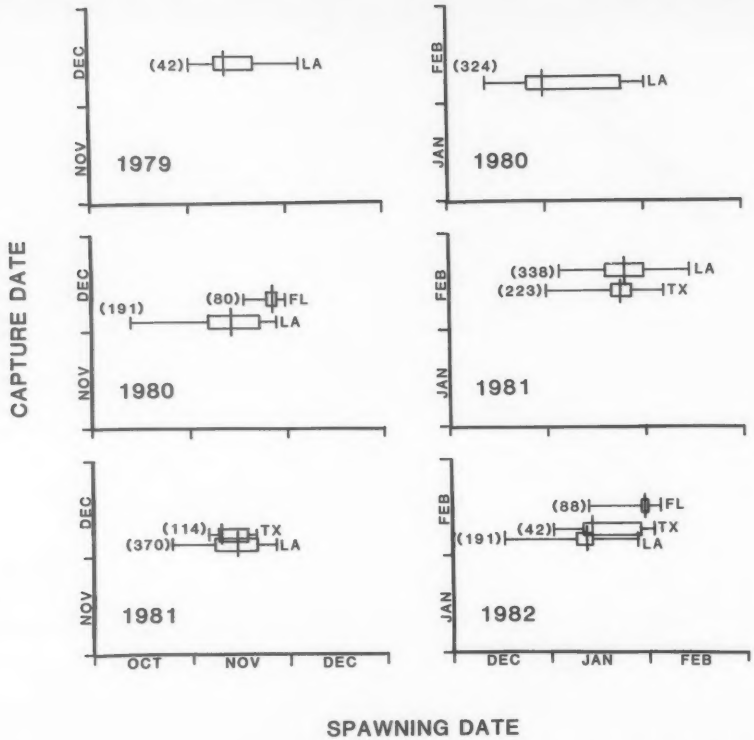

FIGURE 8.—Schematic plots of the spawning times of larval gulf menhaden collected in the northern Gulf of Mexico during 6 cruises of the RV *Oregon II* from December 1979 to February 1982. In each distribution the vertical line is the median value and 50% of the data points fall within the block. Lines beyond the boxes represent the range of data points. The value in parentheses to the left of each distribution is the number of fish.

mouths and were 4.5 mm SL. However, developmental rates are probably temperature dependent (Powell and Phonlor 1986), and hence larvae at lower temperatures would be older at first feeding.

The Gompertz growth model appears to adequately describe the growth of larval gulf menhaden in most cases. Except where data are somewhat limited (Figs. 6b, d; 7b, d) the fit of the model is relatively good and the r^2 is >0.73 for each transect (Table 2). Gompertz growth models have been used (Zweifel and Lasker 1976; Methot and Kramer 1979; Laroche et al. 1982; Warlen and Chester 1985) to describe growth of larval fishes where the length-age plots are nonlinear and upper asymptotes were apparent.

Average growth rate of larval gulf menhaden to day 60 was 0.30 mm/day throughout its oceanic existence. This rate was very similar to that, 0.28 mm/day (estimated from figure 2 of Hettler 1984), for larvae reared in the laboratory at 20° ± 2°C for 60 days. However, wild-caught larvae were from wider extremes in water temperature, with mean early season (December) temperatures from 17.4° to 21.2°C and late season (February) 12.9° to 16.4°C. The growth rate of larval Atlantic herring, *Clupea harengus*, up to 50 days old was similar and varied between 0.23 and 0.30 mm/day (Lough et al. 1982). However, gulf menhaden larvae grew slower than the fast growing but relatively short-lived engraulids—bay anchovy, *Anchoa mitchilli* (Fives et al. 1986) and northern anchovy, *Engraulis mordax* (Methot and Kramer 1979).

Only a small number of larvae from all the collections were ≥50 days old. Larvae of this age

were either not in the sampling area or were inaccessible to the fishing gear used. Although the latter cannot be fully discounted, the former possibility is most likely, since larvae as they grow are known to be transported (Shaw et al. 1985b) toward estuaries. Larvae are about 15–25 mm SL (estimated from Suttkus 1956) when they enter estuaries in Louisiana, and the smallest immigrating larvae are estimated from the growth model (Fig. 4) to have been at least 30 days old. Larvae then are probably 30–70 days old when they enter Gulf of Mexico estuaries. This range is very similar to that for Atlantic menhaden, *B. tyrannus*, entering North Carolina estuaries (S. M. Warlen, unpubl. data). The so-called "larval drift" period for gulf menhaden is probably closer to 4–10 weeks than the 3–5 weeks surmised by Reintjes (1970).

Growth of larval gulf menhaden in the northern Gulf of Mexico varied both spatially and temporally. For three consecutive years there were significant differences in growth for early season (December) and late season (February) larvae caught off the Mississippi River Delta. The increase in length for early season larvae was greater than for larvae hatched in late season. Environmental conditions in this area differed between early season and late season. Mean water temperature measured during the December 1979, 1980, and 1981 cruises were 17.4°, 19.4°, and 21.2°C, respectively, while in February 1980, 1981, and 1982 the temperatures were 13.8°, 15.7°, and 14.7°C, respectively. Although not shown experimentally for gulf menhaden larvae, there is evidence that larvae of some marine fishes grow faster at higher temperatures (Laurence 1978; Laurence et al. 1981). Jones (1985) also associated higher water temperatures with higher growth of larvae and found that increase in length of Atlantic herring larvae hatched early in the season was greater than for larvae hatched late in the season.

Growth rate of larvae caught in the same season but in different years was inversely related to mean water temperature. Larvae caught in December off Louisiana showed a trend of higher growth (1981 < 1980 < 1979) at lower respective mean water temperatures (21.2°, 19.4°, 17.4°C); similarly, the growth rates for larvae caught in February (1981 < 1982 < 1980) was higher at lower respective mean water temperatures (15.7°, 14.7°, 13.8°C). Other environmental factors in addition to temperature may also affect the growth rate of larval menhaden. Food availability that can be an important growth-limiting factor for larval fishes, may be determining the relative growth rates at the lower temperatures in February. On the basis of limited data on the zooplankton (pelecypod larvae, copepod nauplii, copepodites, and adult copepods) that could serve as food for gulf menhaden larvae (Govoni et al. 1983), food availability (number/100 m^3) is highest in February 1980, lower in 1982, and lowest in 1981. Analogous food abundance data is not available for the December cruises, but levels would probably need to be higher on a per fish basis to support the higher metabolism concomitant with the higher December mean water temperatures (17.4°–21.2°C). The main and interaction effects of growth-limiting (food abundance) and growth-regulating (temperature) factors on larval gulf menhaden growth still must be determined experimentally, preferably using laboratory-spawned and -reared larvae.

The apparent growth advantage enjoyed by menhaden larvae spawned early in the season (November) is only typical for a small part of the population. The largest segment of the population, those spawned in the peak months of January and February (Christmas and Waller 1975) and that immigrated to estuaries in February–April, typically had slower growth. Although slower growing, larvae spawned later in the season may be more successful in reaching estuaries. Guillory et al. (1983) found a negative relationship between temperature and gulf menhaden recruitment into Louisiana estuaries. The larger estuarine recruitment later in the season may be related to winter-early spring (January-April) predominant west-northwest longshore flow of coastal water within and just outside the coastal boundary front producing longshore advective transport and of lesser importance by episodic, short-term cross-shelf advection associated with cold fronts (Shaw et al. 1985b). They hypothesized that longshore currents facilitated the movement of larvae toward shore. Only for December did they note a reverse flow (eastward) that would not allow larvae to be transported toward estuaries west of the Mississippi delta.

The between transect comparisons of growth rate of larvae caught off Texas and Louisiana in February showed a difference in 1981 but not in 1982. Again higher growth rates were associated with higher mean water temperatures. Larvae from the LA February 1981 sample ($\bar{x}$ water temperature = 15.7°C) grew faster than larvae from the TX February 1981 sample ($\bar{x}$ water tempera-

ture = 12.0°C). Where no significant differences in growth were found, i.e., between LA and TX February 1982 samples, the respective mean water temperatures were 14.7° and 14.4°C. Neither of those growth curves were significantly different from the curve for larvae from the FL February 1982 sample where the mean water temperature was 16.4°C. However, the paucity of larvae >23 days old caught off Florida in February 1982 (Fig. 7d) suggests that comparisons of that data set with the data sets for larvae caught off Louisiana and Texas in February 1982 would be of little value.

The estimated spawning period for gulf menhaden extended from mid-October to mid-February (Fig. 8). These results agree with Fore (1970) and Christmas and Waller (1975) who, using the occurrence of eggs and larvae, estimated that gulf menhaden spawned from mid-October through March. Gonad weight-body weight ratios of adults (Lewis and Roithmayr 1981) and morphological and physiological features of ovarian tissue (Combs 1969) also indicate that spawning extends from October to early March. Based on the movement of late larvae into Lake Pontchartrain, Suttkus (1956) presumed that gulf menhaden spawning began in October and ceased in February. He suggested that the beginning and end of the spawning period fluctuates from year to year, and that there is no spawning activity during the spring and summer months as Higham and Nicholson (1964) have reported for the closely related Atlantic menhaden.

Most larvae caught in December were spawned in November (Fig. 8) regardless of the year. Larvae caught in February were spawned mostly in January but estimated spawning dates extended from mid-December to mid-February. For any given cruise, larvae from off Texas and Louisiana were spawned at about the same time. There was also considerable overlap in the spawning dates in any cruise off Florida and the other areas. The distribution of the central 50% of spawning dates from the Louisiana sample in February 1980 extended over a 29-d period and was wider than for any other data set. This unusually wide distribution may have been due to the presence of two distinct cohorts, one spawned in late December and one in late January, collected on the February 1980 cruise. Combs (1969) found that this species had intermittent total spawning. Lewis and Roithmayr (1981) inferred that gulf menhaden were intermittent, or fractional spawners. Christmas and Waller (1975) noted a modal temporal distribution of eggs in the region from the Mississippi delta to east of Cape San Blas. Baldauf[4] sampled young menhaden in the lower Neches River, TX, from November through April and found two incoming populations from which he suggested that there may have been two spawning peaks. Only in the larval collections of December 1981 did spawning date distribution appear to be bimodal; 7 and 20 November for Louisiana and 8 and 19 November for Texas. Future sampling throughout the spawning season will be necessary to determine the seasonal periodicity and peaks of gulf menhaden spawning. Relative numbers of larvae in cohorts within the spawning season could then be compared with measurements of environmental conditions as a test of the match-mismatch hypothesis (Cushing 1975) and to further test, as Methot (1983) has done, whether larvae spawned during favorable environmental periods constitute the greatest percentage of the year class.

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SOURCES OF VARIATION IN CATCH PER UNIT EFFORT OF YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA* (STORER), HARVESTED OFF THE COAST OF NEW ENGLAND

LORETTA O'BRIEN AND RALPH K. MAYO[1]

ABSTRACT

Factors affecting variability in commercial catch per unit effort (CPUE) of yellowtail flounder were examined in order to establish a basis for standardizing fishing effort. Analysis of variance (ANOVA) procedures were employed to test for differences in CPUE among vessel tonnage class, fishing area, and depth zone and the interactions between tonnage class and area, and tonnage class and depth. Vessel tonnage class and fishing area accounted for highly significant ($P < 0.01$) sources of variation in CPUE whereas depth was not significant ($P > 0.05$) in most cases. Interactions between tonnage class and stock area were also highly significant in all cases. A series of annual fishing power coefficients was computed for each tonnage class relative to a standard for each stock based on parameter estimates obtained by fitting the CPUE observations to a linear model with tonnage class as the independent variable. Deviations of annual fishing power coefficients from the 20-year mean were found to exhibit significant first order autocorrelations. Consequently, annual coefficients were computed over the entire 1964–83 period by incorporating tonnage class, annual and seasonal effects as independent variables in a three-way linear model. Although the standardized CPUE estimates obtained from this procedure are similar to those obtained by previous methods, the revised procedures described in this paper insure adequate representation of all vessel classes engaged in the yellowtail fishery in the CPUE calculations.

Fishing effort and resulting catch per unit effort (CPUE) indices are routinely used in assessing the impact of commercial fishing operations on stock abundance. The traditional concept that aggregate CPUE indices may be used to measure annual changes in relative stock abundance is based on the principal assumption that the catchability coefficient (q) either remains constant over all fleet components, or that nominal effort is adjusted to account for differences in relative efficiencies (Pope and Parrish 1964; Kimura 1981). Variation in q may be due to persistent differences in fishing power of various types of gear or to technological innovations which may be gradually introduced over time (Gulland 1964; Sissenwine 1978). Biological interactions such as changes in availability of a species due to seasonal distribution patterns or to annual changes in abundance may also affect the overall catchability of demersal species (Garrod 1964; Pope and Garrod 1975). Variability in catchability coefficients may be taken into account by relating nominal fishing effort of each fleet component to some chosen standard category.

Numerous authors have described the basic procedures for calculating relative fishing power of various fleet components. Beverton and Holt (1957) provided evidence to suggest that the distribution of logarithms of fishing power factor/vessel tonnage ratios could be described by a normal curve while Gulland (1956) employed an analysis of variance (ANOVA) model of log CPUE. The properties of the ANOVA model were further examined by Robson (1966) who extended the techniques developed by Gulland (1956) and formally specified the analysis of Beverton and Holt (1957) as a two-way multiplicative ANOVA model. Stern and Hennemuth (1975) employed the method of Robson (1966) in their analysis of fishing effort in the U.S. Georges Bank haddock fishery using depth fished and vessel tonnage as classification variables. In a previous study, Rounsefell (1957) computed standardized log CPUE indices to determine relative abundance of several co-occurring species on Georges Bank according to depth. More recently, Gavaris (1980) and Kimura (1981) have developed modifications of the ANOVA model to estimate annual standardized CPUE indices from time series of catch and effort data by incorporating a year effect in the model.

Standardized annual CPUE indices based on

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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criteria established by Lux (1964) have been routinely used to monitor relative abundance of three stocks of yellowtail flounder, *Limanda ferruginea* (Storer), in the commercial fishery off the New England coast (Fig. 1). Lux calculated CPUE indices for otter trawlers ranging from <26 gross registered tons (GRT) to 100 GRT based on trips in which yellowtail flounder accounted for 50% or more of the total landed weight between 1942 and 1961. A fishing power coefficient was then computed for each of several GRT categories as the ratio of CPUE to a standard GRT category CPUE for the entire timespan. A separate set of fishing power coefficients was computed for each of the three stocks. Lux's (1964) work improved upon an earlier analysis of yellowtail flounder CPUE by Royce et al. (1959) which was based only on relatively small vessels ranging in size from 5 to 50 GRT that dominated the fishery during the 1940's.

Since 1964, numerous technological innovations have drastically changed the character of the New England fishing fleet as traditional side trawlers have gradually given way to larger, more efficient stern trawlers equipped with sophisticated electronic navigation and hydroacoustic devices. This gradual alteration in the fleet characteristics over time suggests that previously documented relationships among vessel categories may no longer be applicable to the current fishery, and that use of nominal effort in CPUE calculations will tend to overestimate relative abundance in the more recent years (Westrheim and Foucher 1985). Long-term declines in yellowtail flounder abundance on each of the principal fishing grounds (Clark et al. 1984) also indicate that current catchability coefficients may differ from previous values. Accordingly, updated fishing power coefficients are required to adequately assess changes in effective fishing effort and CPUE which have occurred during the past two decades. Further, to obtain annual effort and CPUE estimates over such a broad period of years, techniques for computing relative fishing power should incorporate a time element in the analysis.

In this paper we examine variation in CPUE with respect to fishing area, depth, vessel tonnage class, season, and year for three stocks of yellowtail flounder on Georges Bank, Southern New England, and Cape Cod grounds between 1964 and 1983. Before evaluating differences in relative fishing power among vessel classes, we investigate potential interactions between tonnage class and area and tonnage class and depth within each year, and partition the data to minimize tonnage class-area interactions. For each stock, fishing power coefficients are examined for

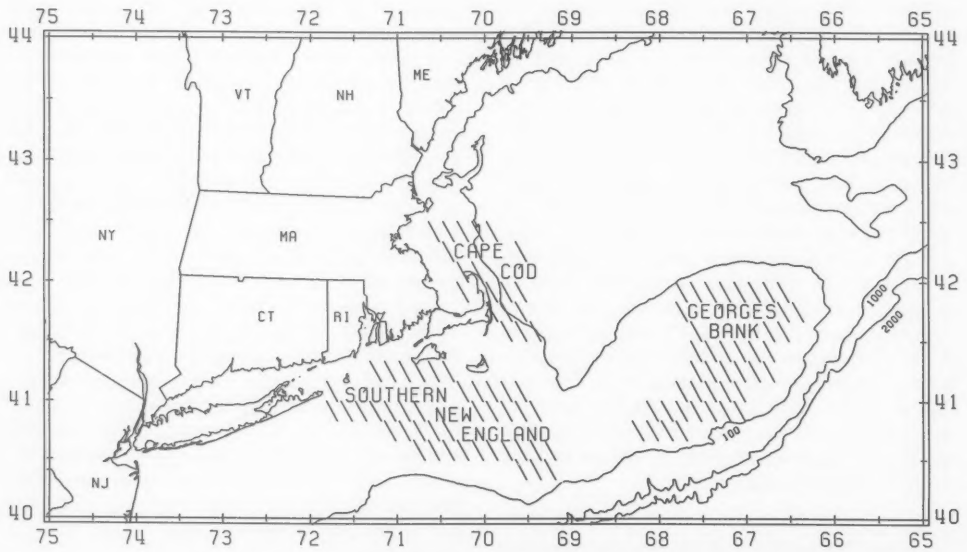


FIGURE 1.—Yellowtail flounder stocks off the coast of New England (After Lux 1963).

annual and seasonal interactions. A three-way linear model, incorporating annual and seasonal components, is employed to compute relative fishing power coefficients over the entire 20-yr period and estimate annual standardized CPUE indices.

DISTRIBUTION OF CATCH AND EFFORT

Commercial exploitation of yellowtail flounder began in the late 1930's following the decline of the winter flounder fishery (Royce et al. 1959). Nominal catches[2] for the three grounds combined rapidly increased to 31,500 metric tons (t) in 1942 but subsequently declined to 5,500 t in 1954. Landings by U.S. vessels gradually increased to a record high of 36,900 t in 1963, but declined again to 10,500 t in 1978 (Fig. 2). Distant water fleet (DWF) catches were also substantial during this period, peaking at 20,700 t in 1969. Overall catches from the three fishing grounds have recently increased to 30,800 t in 1983, although 1984 landings declined to 15,500 t (Clark et al. 1984). The decline in catch during the 1940's was not due to overfishing (Royce et al. 1959) but may have been related to a warming trend in the region which affected recruitment (Sissenwine 1974). The more recent decline between 1969 and 1978, however, has been attributed to increased fishing effort by both domestic and distant water fleets (Brown et al. 1980).

In the early 1940's the size of vessels fishing for yellowtail flounder varied from 5 to 75 GRT. The predominant vessels on Southern New England and Cape Cod grounds ranged from 26 to 50 GRT; on Georges Bank, the dominant vessels were in the 51–75 GRT range. By the mid-1960's larger vessels had begun to enter the fishery, increasing the maximum size to 215 GRT. During this period the size range of the dominant vessels on Southern New England grounds and on Georges Bank had increased to 51–72 and 73–104 GRT, respec-

[2]Nominal catch defined as live weight equivalent of landings, excluding discards.

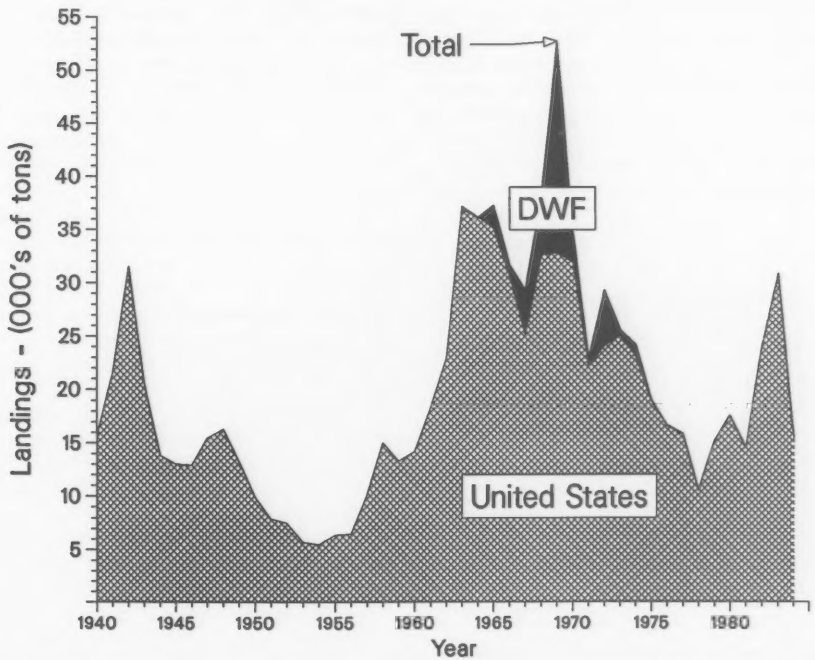


FIGURE 2.—Yellowtail flounder landings (metric tons) by United States and distant water fleet (DWF) vessels from the combined Georges Bank, Southern New England, and Cape Cod grounds, 1940–84.

tively. Vessels fishing the relatively nearshore Cape Cod grounds remained in the 34–50 GRT range. Larger vessels continued to enter the fishery during the 1970's and, by 1983, several vessels were in the 311–400 GRT range. Since 1964, vessel GRT's have been categorized by tonnage class (TC) as given in Table 1a.

A review of Lux's (1964) data from 1942 to 1961 and the distribution of more recent yellowtail flounder landings from 1964 to 1983 (Figs. 3–5) reveal that vessels of similar size have continually fished the same general areas over the past 40 years. The TC 21–24 vessels fish primarily on Southern New England and Cape Cod grounds (Fig. 3), although TC 24 vessels occasionally enter the southwest part of Georges Bank. The TC 25–33 vessels fish on both Georges Bank and Southern New England grounds (Fig. 4), while TC 41–43 vessels concentrate on Georges Bank (Fig. 5). Although TC 41 vessels operate at times on the eastern part of the Southern New England grounds, the TC 42 and 43 vessels fish exclusively on Georges Bank.

The distribution plots (Figs. 3–5) reveal a gradual phaseout of smaller (TC 21–24) vessels on the inshore Southern New England and Cape Cod grounds and a concurrent increase in the activity of large (TC 41–43) vessels on Georges Bank, Southern New England, and, to a lesser extent, on the Cape Cod grounds. In evaluating trends in CPUE we must ask whether these changes in the yellowtail fishery over the past 20 years (i.e., the shift in the predominant vessel size on two of the three grounds and the addition of larger vessels to the fleet on all three grounds) affect CPUE as calculated by the traditional method (Lux 1964). If the same size range of vessels (5–100 GRT) had fished for yellowtail flounder throughout the years, a shift in the dominant vessel class would not affect CPUE estimates since effort would be standardized against the same class and is, therefore, relative. However, the maximum vessel size has increased and the predominant TC now represents vessels larger than 100 GRT. Since landings and effort data contributed by these larger vessels were not incorporated into previous CPUE calculations, CPUE estimates will not necessarily represent overall fleet performance in recent years. The following procedures, therefore, were developed to calculate new fishing power coefficients that encompass the entire size range of vessels currently in the fishery.

TABLE 1.—Definition of vessel tonnage classes (a) and depth ranges and corresponding zones (b) included in analysis of variance of yellowtail flounder CPUE.

a	Gross registered tonnage (range)	Vessel tonnage class
	5–10	21
	11–15	22
	16–22	23
	23–33	24
	34–50	25
	51–72	31
	73–104	32
	105–150	33
	151–215	41
	216–310	42
	311–400	43
b	Depth range (m)	Depth zone
	1–55	1
	56–110	2
	111–183	3

METHODS OF ANALYSIS

Catch and effort data recorded by trip were obtained from Northeast Fisheries Center (NEFC) detailed commercial landings files. Fishing effort or days fished (df) is defined on a 24-h basis as number of hours of actual fishing time divided by 24. Only trips landing 50% or more of yellowtail flounder were analyzed; trips included within the qualification level generally accounted for 70–90% of the total yellowtail landings over the entire period, except on Cape Cod grounds where qualified trips accounted for 40–60% of the total. Catch per day fished (CPUE) was computed for each trip and transformed to ln CPUE since preliminary analysis indicated a positive correlation of the arithmetic mean CPUE with the variance. Use of the log transformation, however, stabilized the variance and created a lognormal distribution as noted by Gulland (1956) and Steel and Torrie (1980).

Trips landing between 1964 and 1983 are classified in the data base by vessel tonnage class, statistical area, and depth zone fished. Vessels ranging in size from 5 to 310 GRT (Table 1a) and statistical areas corresponding to the three major stocks were selected for analysis as follows: Georges Bank (areas 522–525), Southern New England (area 526 and 537–539), and Cape Cod (areas 514 and 521) (Fig. 6). Because of their sporadic representation, TC 21–23 vessels have been excluded from the Georges Bank analyses and have been combined as one category on the Southern New England grounds. Depth zones 1, 2, and

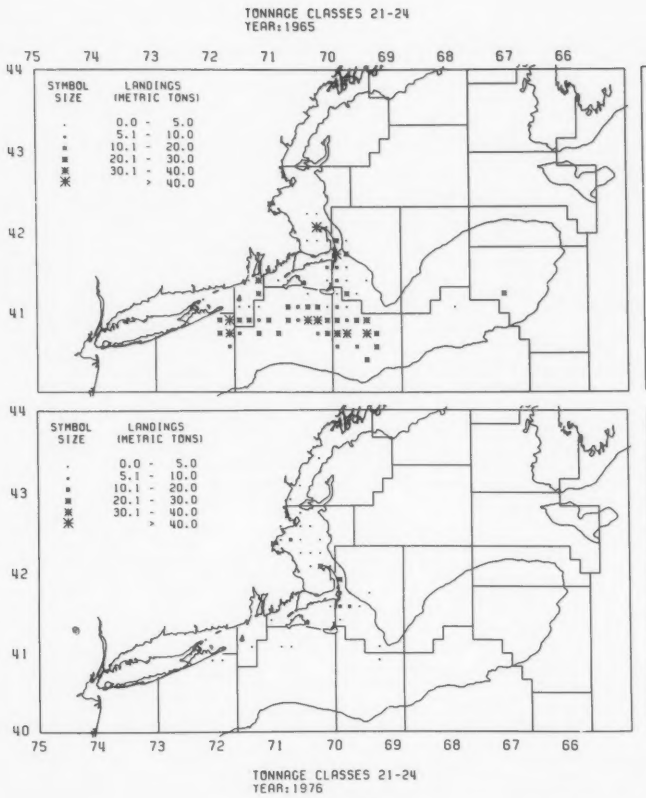
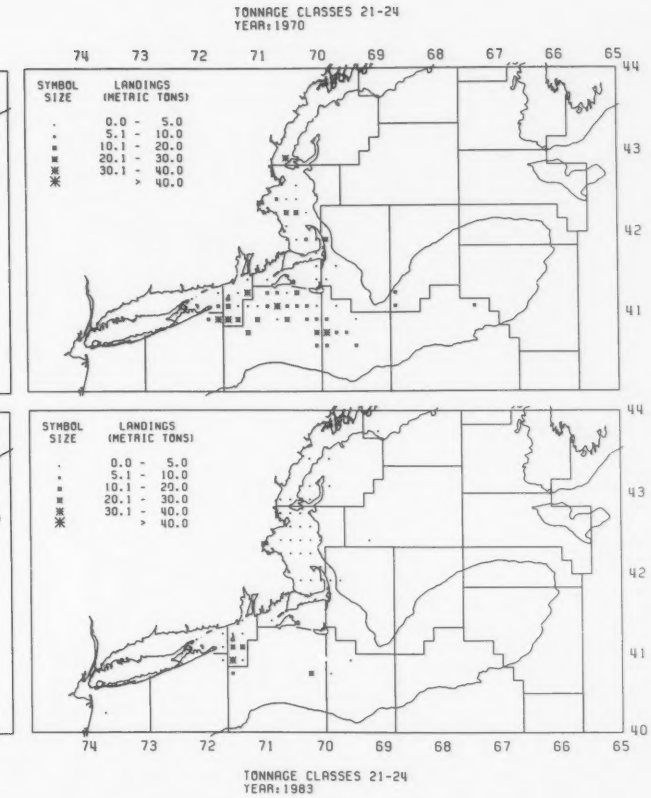


FIGURE 3.—Distribution of yellowtail flounder landings in 19



in 1965, 1970, 1976, and 1983 for vessel tonnage classes 21–24.

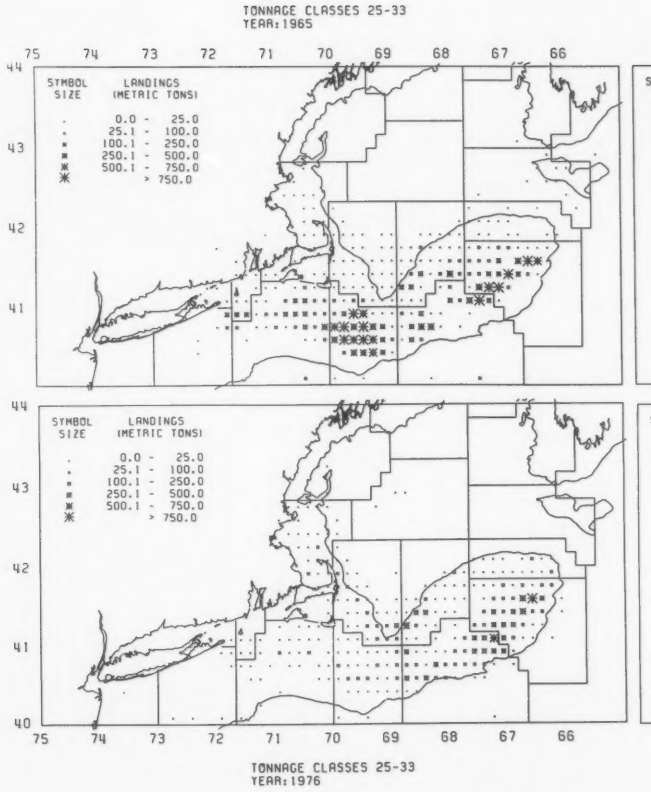
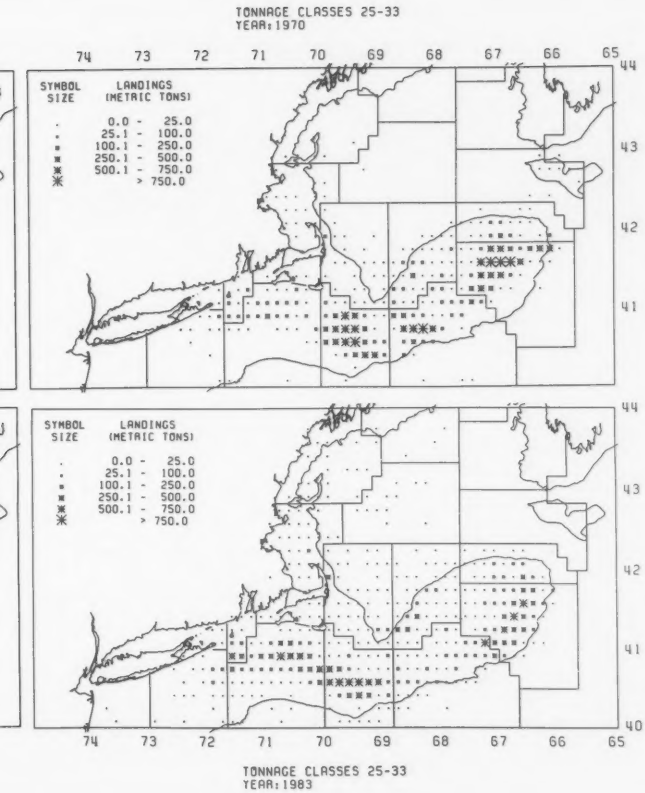


FIGURE 4.—Distribution of yellowtail flounder landings in 196



in 1965, 1970, 1976, and 1983 for vessel tonnage classes 25–33.

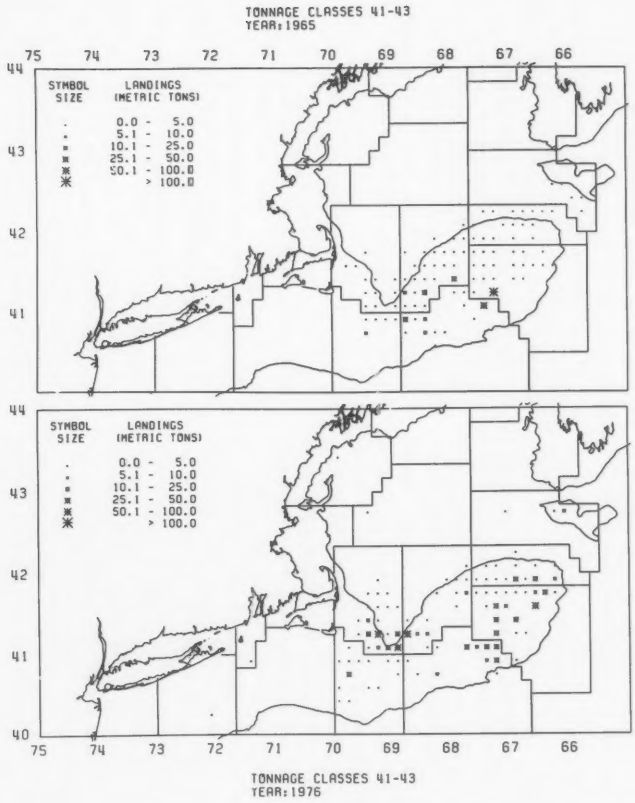
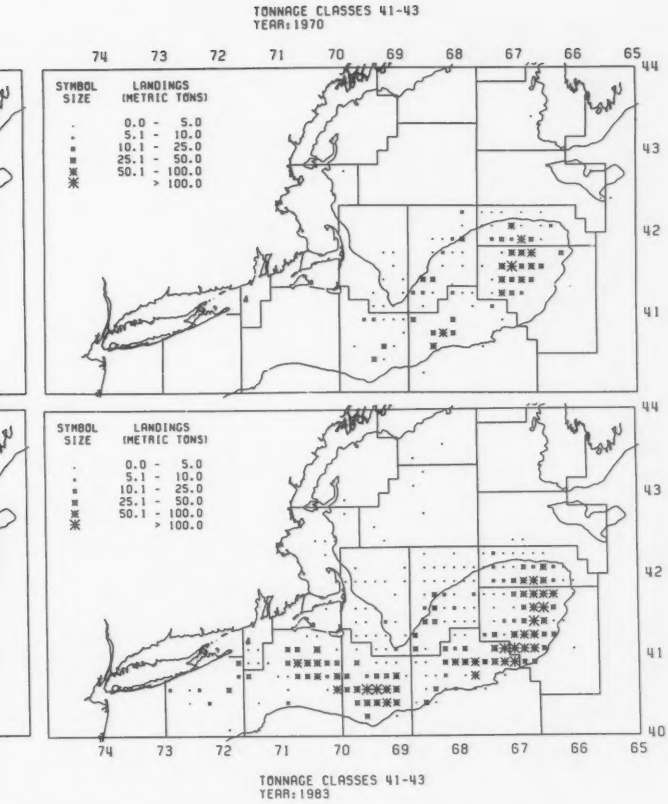


FIGURE 5.—Distribution of yellowtail flounder landings in



ngs in 1965, 1970, 1976, and 1983 for vessel tonnage classes 41–43.

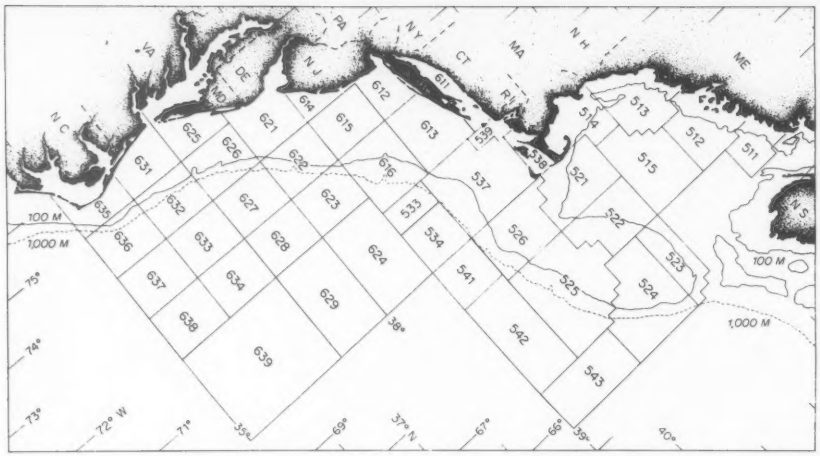


FIGURE 6.—Yellowtail flounder fishing grounds defined by U.S. statistical area are as follows: Southern New England, 526–539; Georges Bank, 522–525; Cape Cod, 514 and 521.

3 (Table 1b) were also selected from six possible zones based on the bathymetric distribution of yellowtail flounder.

Trip data were aggregated at different levels of spatial resolution to examine variability in CPUE over the entire region and within each of the three established stocks. Two-way ANOVAs with interaction were performed on annual data sets using the BMDP statistical software program P4V (Dixon 1981). Given the large number of observations in each analysis, the more rigorous 99% significance level was chosen to test the null hypothesis (no significant differences) since relatively small differences in mean CPUE can produce statistically significant results. The ANOVA was performed initially to test for differences in CPUE among all tonnage classes and statistical areas and to determine the overall extent of tonnage class-area interactions. Secondary analyses were performed to examine the effect of tonnage class-area and tonnage class-depth interactions among and within each of the stocks. All subsequent tests for significance of tonnage class, area, and depth main effects were performed with the interaction effects absorbed in the error sum of squares. Estimates of annual geometric mean CPUE were obtained by combinations of tonnage class, stock area, and depth from the row and column means provided by the P4V software (Tables 2, 3).

A standard vessel class was selected for each of the three stocks for use in calculation of fishing power coefficients based on the prevalence of the vessel class in the fishery and its relative contribution to the landings over the 20 years. The TC 32 category was chosen as the standard for both Georges Bank and Southern New England stocks, and the TC 25 class was chosen as the standard for the Cape Cod stock. Within each stock annual fishing power coefficients were derived for each tonnage class relative to the standard by fitting ln CPUE to a one-way linear model using the GLM procedure of the Statistical Analysis System (SAS Institute 1982) as follows:

$$U = \alpha + \sum_j [\beta_j X_j] + \epsilon.$$

Annual deviations of the coefficients from the 20-yr mean were tested for first order autocorrelation using the Durbin-Watson test statistic (Neter and Wasserman 1974). A time component was subsequently incorporated in the linear model to account for annual trends in the data; seasonal effects were also included by classifying the data according to calendar quarter. The initial year (1964) and the fourth quarter were selected as reference categories. The general model is specified as:

TABLE 2.—Geometric mean CPUE[1] (landings per day fished, metric tons) for Georges Bank, Southern New England, and Cape Cod yellowtail flounder trips by vessel tonnage class, 1964–83.

Year	Vessel tonnage class									
	21	22	23	24	25	31	32	33	41	42
Georges Bank										
1964	—	—	—	3.65	4.17	4.88	5.04	4.58	4.52	2.14
1965	—	—	—	2.41	3.06	3.62	3.55	3.39	4.97	—
1966	—	—	1.18	1.25	2.27	2.76	2.78	2.76	2.71	—
1967	—	—	—	—	2.20	2.74	2.96	2.78	2.65	—
1968	—	—	—	3.88	2.99	3.47	3.55	3.84	3.53	2.66
1969	—	—	—	3.28	2.82	3.06	3.30	3.02	2.81	3.88
1970	—	—	—	3.74	2.40	2.88	3.08	2.81	2.70	—
1971	—	—	—	1.66	2.07	2.70	2.52	2.24	2.35	—
1972	—	—	—	—	1.96	2.24	2.39	2.29	1.96	—
1973	—	—	—	1.38	2.64	2.61	2.81	3.05	2.76	3.20
1974	—	2.52	—	—	2.79	2.13	2.23	2.19	1.30	3.42
1975	—	—	—	1.93	1.91	1.64	1.93	2.04	1.72	3.19
1976	—	—	—	1.35	1.69	1.77	1.84	2.16	2.06	—
1977	—	—	—	—	1.17	1.66	1.77	2.26	1.81	—
1978	—	—	—	—	1.67	1.50	1.72	2.03	2.82	—
1979	—	2.69	—	1.31	1.80	2.41	2.37	2.82	3.64	—
1980	—	0.30	—	1.09	0.90	2.88	2.62	3.27	3.00	—
1981	—	—	—	1.12	1.24	1.98	2.48	2.61	2.23	—
1982	—	—	1.88	0.48	2.02	1.71	2.10	2.53	3.97	2.07
1983	—	—	—	—	0.79	2.46	1.97	2.21	3.79	—
Southern New England										
1964	2.34	1.94	6.15	4.88	4.66	4.44	5.04	4.59	4.09	—
1965	1.77	1.55	3.87	3.62	3.12	3.56	3.81	4.05	1.50	—
1966	1.21	3.06	3.19	2.93	2.52	2.61	2.56	2.35	3.03	—
1967	1.80	1.14	2.94	3.38	3.23	2.67	2.66	2.31	1.80	—
1968	2.24	4.15	4.69	4.42	4.02	3.41	3.62	3.63	3.53	—
1969	2.65	3.72	5.17	3.81	4.10	3.39	3.43	4.01	2.81	—
1970	7.74	3.28	4.76	3.77	3.96	3.08	3.64	2.87	2.70	—
1971	11.72	1.60	4.06	3.14	3.32	2.85	2.87	3.16	2.35	—
1972	—	1.96	3.19	2.62	3.30	3.01	2.96	3.04	1.96	—
1973	—	1.01	1.05	2.26	2.66	2.29	2.22	2.12	2.76	—
1974	—	1.08	1.62	2.31	2.14	2.07	2.07	2.64	1.30	—
1975	—	0.57	1.57	1.13	1.29	1.33	1.55	1.55	1.72	—
1976	—	0.72	0.90	0.53	0.86	1.13	1.32	1.69	2.06	—
1977	—	0.93	1.73	1.44	1.77	1.61	1.82	1.98	1.81	—
1978	—	—	2.72	1.15	1.58	1.52	2.04	2.26	2.82	—
1979	0.79	1.74	2.28	1.59	2.17	2.32	2.93	2.88	3.64	—
1980	—	1.02	2.46	1.91	2.54	2.68	2.81	3.07	3.00	—
1981	—	1.88	2.50	1.43	2.58	2.76	2.61	3.28	2.23	—
1982	2.49	1.96	2.42	2.29	3.10	3.20	3.72	3.98	3.97	—
1983	8.81	1.74	2.51	3.35	3.43	3.27	3.65	3.57	3.79	—
Cape Cod										
1964	—	1.65	1.38	1.94	2.64	2.85	2.76	—	—	—
1965	—	1.45	1.20	1.59	2.16	3.56	2.12	2.07	—	—
1966	1.13	1.07	1.23	1.48	2.55	3.64	1.76	—	—	—
1967	—	0.78	0.90	1.56	2.46	3.21	1.95	2.62	—	—
1968	—	1.16	0.99	1.89	2.65	4.11	2.42	—	1.13	—
1969	—	1.66	1.33	2.02	2.77	3.64	2.47	—	—	—
1970	—	1.03	1.05	2.34	2.33	3.64	[2]6.96	[2]34.18	2.91	—
1971	—	1.17	1.89	2.43	2.04	2.24	1.90	2.45	3.36	—
1972	1.71	1.63	1.16	2.02	1.85	2.02	1.46	1.79	1.93	—
1973	1.02	1.32	1.06	1.87	1.99	1.90	1.91	1.63	2.84	—
1974	0.83	1.15	0.90	1.59	2.08	1.74	1.82	1.87	1.37	—
1975	0.77	1.13	1.23	1.42	1.92	1.45	1.64	1.09	1.19	—
1976	0.34	1.31	1.38	1.69	1.93	1.42	1.54	1.88	2.15	—
1977	0.28	0.86	1.25	1.50	2.03	1.45	1.42	2.19	2.57	—
1978	—	0.84	1.59	1.90	2.11	1.96	1.53	1.92	5.99	—
1979	0.98	0.91	1.42	1.83	2.10	2.24	1.74	2.23	3.12	—
1980	0.26	0.58	1.30	1.73	2.18	2.24	2.07	2.19	3.34	—
1981	0.70	0.76	1.17	1.69	2.24	2.40	1.22	1.85	2.99	—
1982	0.54	0.71	1.22	1.79	2.02	2.41	1.57	1.94	2.37	—
1983	0.69	1.51	1.23	1.96	1.91	1.29	1.53	1.46	0.83	—

[1]Calculated as $\exp\left[1/n \cdot \Sigma \ln\left(\frac{\text{landings}}{\text{effort}}\right)\right]$

[2]Only one trip by tonnage classes 32 and 33 in 1970 on Cape Cod grounds.

$$U = \alpha + \sum_{ij} [\beta_{ij} X_{ij}] + \epsilon$$

where U = ln CPUE,

α = intercept estimate,

β_{ij} = model parameter estimates in logarithmic units for category j for tonnage class, season, and year,

X_{ij} = dummy variable for tonnage class, season, and year (=1 when category j occurs; = 0 otherwise), and

ϵ = error term.

All tests for significance of main effects were based on the above model without interaction. Separate ANOVAs were also performed to examine first order interactions. Parameter estimates obtained from the model without interaction were retransformed following methods described by Bradu and Mundlak (1970) to derive unbiased fishing power, seasonal, and annual coefficients. Annual coefficients corresponding to the 1965–83 period were multiplied by the reference year CPUE to compute annual standardized CPUE estimates.

RESULTS

Smaller vessels (TC 21–24) generally exhibited the lowest CPUE indices in all three areas, although TC 21–23 vessels were not represented on Georges Bank (Table 2). Catch rates of medium vessels (TC 25; 31–33) were similar to each other, and were generally greater than those for TC 21–24 vessels. Mean CPUE indices for the largest vessels (TC 41 and 42) were more variable, but generally were equal to or greater than those

TABLE 3.—Geometric mean CPUE[1] (landings per day fished, metric tons) for Georges Bank, Southern New England, and Cape Cod yellowtail flounder trips by depth zone, 1964–83.

	Georges Bank				Southern New England				Cape Cod			
	Depth zone				Depth zone				Depth zone			
Year	1	2	3	Combined	1	2	3	Combined	1	2	3	Combined
1964	3.92	4.91	2.74	4.80	5.05	4.96	4.71	5.03	2.13	2.36	—	2.25
1965	3.76	3.48	—	3.55	3.61	3.88	2.28	3.66	1.61	1.80	2.36	1.71
1966	3.02	2.62	1.29	2.71	2.71	2.66	0.71	2.71	1.99	2.13	1.70	2.07
1967	3.19	2.69	2.81	2.79	2.97	2.77	1.14	2.91	1.52	2.16	—	1.80
1968	3.38	3.51	—	3.49	3.70	3.97	3.24	3.76	2.15	2.31	—	2.24
1969	3.36	3.11	—	3.16	3.62	3.93	1.58	3.66	2.16	2.66	—	2.27
1970	2.81	2.99	1.00	2.93	3.44	3.68	1.62	3.49	1.10	2.24	[2]34.18	1.40
1971	2.20	2.30	2.75	2.28	3.26	2.96	—	3.14	1.03	1.94	—	1.46
1972	2.28	2.37	1.34	2.35	3.28	3.25	2.74	3.27	1.56	1.88	—	1.82
1973	2.30	3.06	2.85	2.91	2.41	2.55	4.40	2.47	1.75	1.83	2.27	1.81
1974	2.10	2.32	2.90	2.30	2.31	2.02	—	2.19	1.86	1.78	—	1.82
1975	1.85	1.99	1.29	1.98	1.59	1.63	—	1.60	1.53	1.38	1.32	1.46
1976	1.75	2.06	—	2.03	1.34	1.56	—	1.43	1.54	1.88	2.93	1.70
1977	1.92	2.15	1.67	2.14	1.92	1.97	—	1.94	1.70	1.89	1.27	1.77
1978	1.78	2.09	1.98	2.07	2.45	2.17	—	2.32	1.90	1.71	3.49	1.86
1979	2.47	2.79	2.04	2.74	2.88	2.39	—	2.76	2.03	2.03	2.47	2.03
1980	2.58	3.50	1.53	3.37	2.71	3.51	1.13	3.04	2.06	2.31	2.38	2.16
1981	2.26	2.88	1.54	2.76	2.46	2.78	—	2.58	1.74	1.96	5.67	1.79
1982	2.34	2.66	2.53	2.62	3.20	3.54	4.53	3.31	1.81	1.44	0.91	1.67
1983	1.98	2.28	3.04	2.26	3.08	3.13	5.91	3.10	1.70	1.41	—	1.62

[1]Calculated as $\exp\left[1/n \cdot \Sigma \ln\left(\frac{\text{landings}}{\text{effort}}\right)\right]$.

[2]Only one trip in depth zone 3 in 1970 on Cape Cod grounds.

corresponding to medium and small vessels, particularly in the later years (Table 2). The initial ANOVAs performed over all statistical areas revealed highly significant ($P < 0.01$) differences in CPUE for tonnage class and area main effects in each of the 20 years (Table 4). The interaction of tonnage class and area was also highly significant in all years, suggesting that relative fishing power of the individual vessel classes varies according to area. ANOVA results for the comparison of CPUE among stocks were highly significant for area main effects in 19 out of 20 years, and the tonnage class-stock area interaction term was highly significant in all years (Table 4). Grouping the data according to stock tended to reduce the amount of significant tonnage class-area interaction within each stock, although differences among tonnage classes remained highly significant.

On Georges Bank the differences in CPUE were highly significant for statistical area and tonnage class main effects in 80 and 100% of the years, respectively, while the tonnage class-area interaction was highly significant in only 40% of the years. Differences due to area on Southern New England grounds were highly significant in all years except 1978, and differences due to tonnage class were highly significant in all years. The interaction term was highly significant in 70% of the years. Differences due to area on the Cape Cod grounds were highly significant in all years except 1975, and differences due to tonnage class were highly significant for all years. The interaction was highly significant in only 35% of the years (Table 4).

Differences in CPUE by depth zone were generally not significant. Depth main effects yielded

TABLE 4.—Frequency with which highly significant ($P < 0.01$) results were obtained from analysis of variance (ANOVA) tests of yellowtail flounder annual CPUE data. (Total number of years tested = 20.) N/A = Not applicable (tests not performed).

	Main effects		
	Area	Tonnage class	Depth
All areas	20/20	20/20	N/A
Among stocks	19/20	N/A	N/A
Within stocks			
Georges Bank	16/20	20/20	10/20
So. New England	19/20	20/20	7/20
Cape Cod	19/20	20/20	3/20

	Interactions	
	Tonnage class × area	Tonnage class × depth
All areas	20/20	N/A
Among stocks	20/20	N/A
Within stocks		
Georges Bank	8/20	4/20
So. New England	14/20	2/20
Cape Cod	7/20	1/20

highly significant differences in only 50, 35, and 15% of the years for Georges Bank, Southern New England, and Cape Cod grounds, respectively (Table 4), while the tonnage class-depth interaction was highly significant in no more than 20% of the years on each of the three grounds.

Interaction between tonnage class and statistical area throughout the region was highly significant in all cases. Further analyses yielded highly significant differences in CPUE among the three stocks and highly significant tonnage class-stock interactions which suggests that relative fishing power among vessel classes is not consistent from stock to stock, implying a need for computing a separate set of fishing power coefficients for each stock. Within each stock, differences in CPUE among statistical areas and tonnage classes were also highly significant in most cases, although the tonnage class-area interaction was not.

Standardized CPUE

Annual fishing power coefficients, obtained by retransforming linear model parameter estimates for each tonnage class, are presented in Table 5 by stock. Cursory examination of the coefficients reveals distinct trends throughout the 20-yr series. On Georges Bank and Southern New England grounds, fishing power coefficients for the smaller vessels (TC 23–25) relative to the standard declined over time, whereas coefficients for the larger vessels increased over time. On Cape Cod grounds the coefficients increased for the smaller vessels (TC 23 and 24) although trends were less pronounced. These trends are illustrated graphically by plotting annual deviations from the 20-yr average in Figures 7–9. A Durbin-Watson test for first order autocorrelation of the annual deviations (Neter and Wasserman 1974) was significant for most tonnage classes within each of the stocks, suggesting the presence of a substantial tonnage class-time interaction.

The three-way linear model, modified to include interaction terms, also revealed highly significant tonnage class-year as well as tonnage class-season and year-season interactions within each of the three stocks (Table 6). When interactions are significant, they can be examined in detail or absorbed in the error term when testing for main effects. Since tonnage class effects have already been examined on an annual basis, the interaction terms were excluded from the three-way model used to obtain parameter estimates for tonnage class, season, and year. The model is specified as follows:

$$U = \alpha + \sum_j [\beta_{1j} X_{1j} + \beta_{2j} X_{2j} + \beta_{3j} X_{3j}] + \epsilon$$

where $\beta_{1j}, \beta_{2j}, \beta_{3j}$ = model parameter estimates in logarithmic units for category j for tonnage class, season, and year,

X_{1j}, X_{2j}, X_{3j} = dummy variables for tonnage class, season, and year (= 1 when category j occurs; = 0 otherwise).

ANOVA results obtained without interaction are presented in Table 6 for each of the three stocks. For Georges Bank and Southern New England stocks, year accounts for the greatest reduction in error sums of squares; on Cape Cod grounds tonnage class accounts for the greatest overall reduction.

Coefficients for tonnage class, year, and season, derived from model parameter estimates for the combined 1964–83 period are presented in Table 7. Tonnage class coefficients for Georges Bank and Southern New England are relatively homogeneous, as compared with those obtained for Cape Cod grounds, owing to the narrower range of vessel tonnage classes which have consistently exploited these fisheries. Seasonal coefficients exhibit the same pattern on Georges Bank and Southern New England with the highest catch rates occurring during the third quarter; on Cape Cod grounds the highest catch rates occur during the second quarter. Trends in annual coefficients are similar on all three grounds. Standardized CPUE indices based on the annual coefficients are illustrated in Figure 10, and traditional indices based on the methods of Lux (1964), as given by Clark et al. (1984), are also presented for comparative purposes.

Although each series indicates similar trends, CPUE indices obtained from the linear model for Georges Bank and Southern New England have remained slightly higher than the traditional indices since the early 1970's. Prior to this, the traditional CPUE indices were greater than the revised indices. On Cape Cod grounds, differences between the two series are considerably greater, particularly in the early years.

TABLE 5.—Annual fishing power coefficients calculated by vessel tonnage Georges Bank, Southern New England,

Year	Vessel tonnage class[1]								
	21	22	23	24	25	31	32	33	41	42
				Georges Bank						
1964				0.73	0.83	0.97		0.91	0.90	0.43
1965				0.68	0.86	1.02		0.95	1.40	—
1966				0.45	0.81	0.99		0.99	0.97	—
1967				—	0.74	0.93		0.94	0.89	—
1968				1.09	0.84	0.98		1.08	0.88	0.75
1969				0.99	0.85	0.93		0.92	0.95	1.17
1970				1.21	0.78	0.94		0.91	0.94	0.92
1971				0.66	0.82	1.07		0.89	1.12	—
1972				—	0.82	0.94		0.96	0.93	—
1973		not		0.49	0.94	0.93	1.00	1.09	1.09	1.14
1974		calculated		—	1.25	0.96		0.98	0.97	1.53
1975				1.00	0.99	0.85		1.06	1.04	1.66
1976				0.73	0.92	0.96		1.17	1.01	—
1977				—	0.66	0.94		1.28	1.67	—
1978				—	0.97	0.87		1.18	1.54	—
1979				0.55	0.76	1.02		1.19	1.35	—
1980				0.42	0.35	1.10		1.25	1.43	—
1981				0.45	0.50	0.80		1.05	1.16	—
1982				0.23	0.96	0.82		1.21	1.41	0.99
1983				—	0.40	1.25		1.12	1.26	—
				Southern New England						
1964	—	[2]0.95	—	0.97	0.92	0.88		0.91	0.81	
1965	—	0.86	—	0.95	0.82	0.93		1.06	0.39	
1966	—	1.12	—	1.14	0.98	1.02		0.92	1.18	
1967	—	0.94	—	1.27	1.22	1.00		0.87	0.68	
1968	—	1.21	—	1.23	1.11	0.94		1.01	0.98	
1969	—	1.32	—	1.11	1.19	0.99		1.17	0.82	
1970	—	1.23	—	1.04	1.09	0.85		0.79	0.74	
1971	—	1.06	—	1.10	1.16	0.99		1.10	0.82	
1972	—	0.99	—	0.88	1.12	1.01		1.03	0.66	
1973	—	0.46	—	1.01	1.20	1.03	1.00	0.95	1.24	

[1]Standard vessel class on Georges Bank and Southern New England rounds = 32. Standard vessel class on Cape Cod grounds = 25.

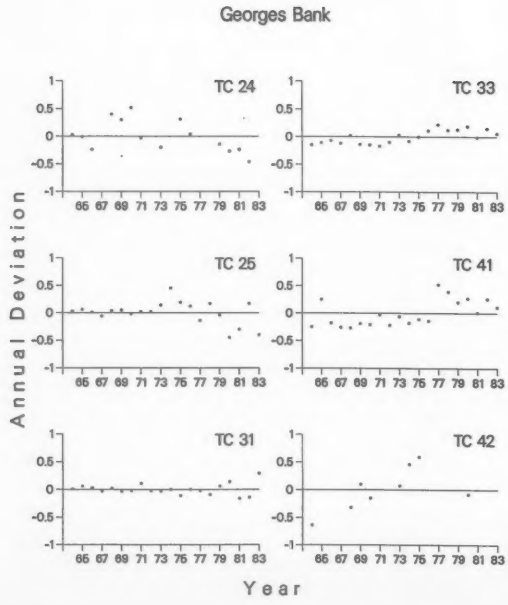


FIGURE 7.—Deviations in annual fishing power from the 1964–83 20-yr mean for major vessel tonnage classes fishing on Georges Bank.

class relative to a standard class vessel fishing for yellowtail flounder on and Cape Cod grounds, 1964–83.

Year	Vessel tonnage class[1]									
	21	22	23	24	25	31	32	33	41	42
				Southern New England						
1974	—	0.67	—	1.11	1.03	1.00		1.27	0.62	
1975	—	0.72	—	0.73	0.83	0.85		1.00	1.11	
1976	—	0.66	—	0.40	0.66	0.86		1.28	1.56	
1977	—	0.87	—	0.79	0.97	0.88		1.09	0.99	
1978	—	1.33	—	0.56	0.78	0.75		1.11	1.38	
1979	—	0.69	—	0.54	0.74	0.79		0.98	1.24	
1980	—	0.82	—	0.68	0.90	0.95		1.09	1.07	
1981	—	0.92	—	0.55	0.99	1.06		1.26	0.86	
1982	—	0.64	—	0.62	0.84	0.86		1.07	1.07	
1983	—	0.68	—	0.92	0.94	0.89		0.98	1.04	
				Cape Cod						
1964	—	0.62	0.52	0.73		1.08	1.04	—	—	
1965	—	0.67	0.55	0.73		1.65	0.98	0.96	—	
1966	0.44	0.42	0.48	0.58		1.42	0.69	—	—	
1967	—	0.32	0.36	0.64		1.30	0.79	1.07	—	
1968	—	0.44	0.37	0.71		1.55	0.91	0.99	0.43	
1969	—	0.60	0.48	0.73		1.31	0.89	—	—	
1970	—	0.44	0.45	1.01		1.56	(3)	(3)	1.25	
1971	—	0.57	0.93	1.19		1.10	0.93	1.20	1.65	
1972	0.93	0.88	0.63	1.09		1.09	0.79	0.97	1.05	
1973	0.51	0.66	0.53	0.94	1.00	0.95	0.96	0.82	1.43	
1974	0.40	0.55	0.43	0.76		0.83	0.87	0.90	0.66	
1975	0.40	0.59	0.64	0.74		0.75	0.85	0.57	0.62	
1976	0.18	0.68	0.72	0.88		0.73	0.80	0.97	1.12	
1977	0.14	0.42	0.61	0.74		0.71	0.70	1.08	1.26	
1978	—	0.40	0.75	0.90		0.93	0.73	0.91	2.84	
1979	0.47	0.43	0.68	0.87		1.06	0.83	1.06	1.48	
1980	0.12	0.27	0.60	0.80		1.03	0.95	1.01	1.53	
1981	0.31	0.34	0.52	0.75		1.07	0.54	0.83	1.34	
1982	0.27	0.35	0.60	0.88		1.19	0.77	0.96	1.17	
1983	0.36	0.79	0.64	1.02		0.68	0.80	0.77	0.43	

[2]Vessel classes 21, 22, and 23 combined on Southern New England grounds.

[3]Insufficient data for these categories.

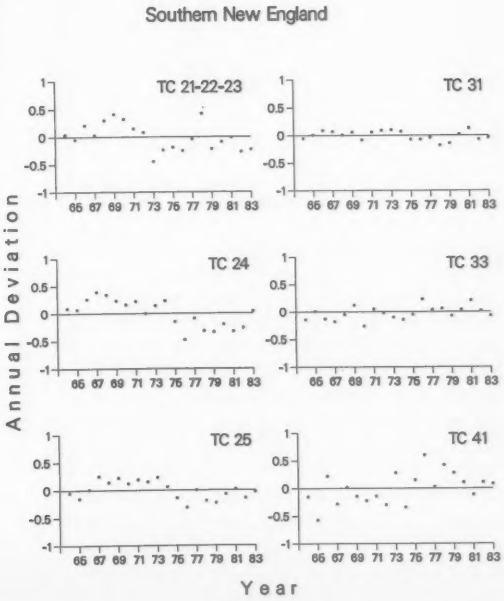


FIGURE 8.—Deviations in annual fishing power from the 1964–83 20-yr mean for major vessel tonnage classes fishing on Southern New England grounds.

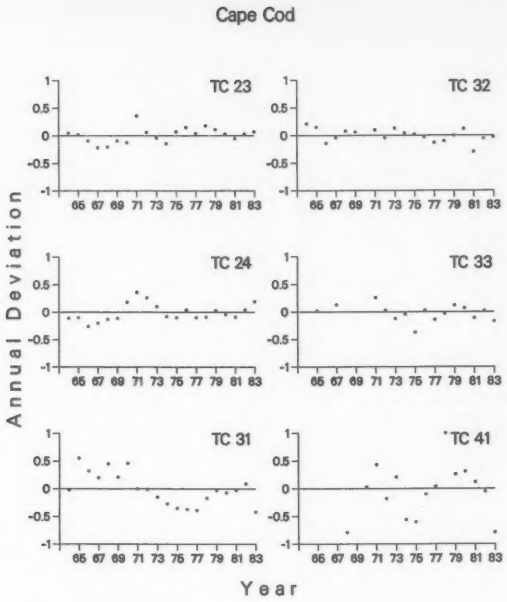


FIGURE 9.—Deviations in annual fishing power from the 1964–83 20-yr mean for major vessel tonnage classes fishing on Cape Cod grounds.

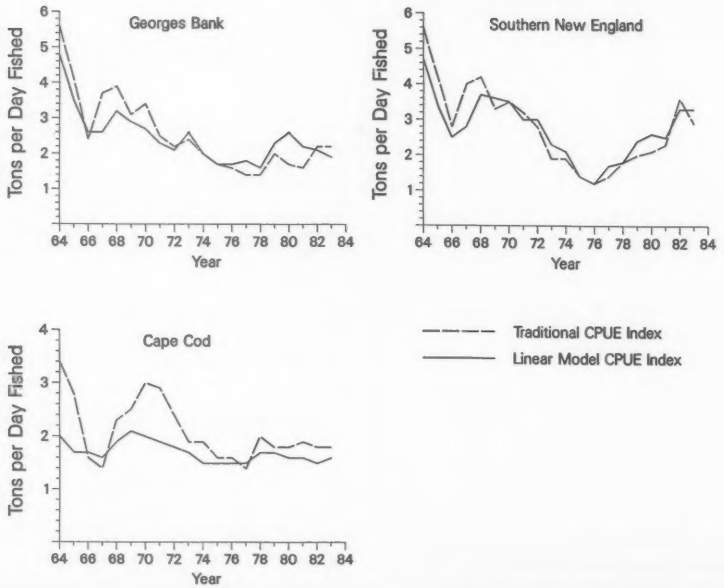


FIGURE 10.—Trends in annual yellowtail flounder CPUE (metric tons per day fished) calculated with traditional CPUE based on Lux (1964) and annual coefficients (linear model CPUE).

TABLE 6.—ANOVA results obtained from a three-way linear model incorporating year, quarter, and tonnage class for Georges Bank, Southern New England, and Cape Cod stocks of yellowtail flounder.

Source	df	Sum of squares	Mean square	F value	P
Georges Bank					
With interaction					
Model	211	1,432.92	6.79	29.53	<0.01
Year	19	908.42	47.81	207.88	<0.01
Qtr	3	107.36	35.79	155.59	<0.01
TC	9	84.24	9.36	40.70	<0.01
Yr*Tc	103	116.81	1.13	4.93	<0.01
Yr*Qtr	57	202.29	3.55	15.43	<0.01
Qtr*Tc	20	13.80	0.69	3.00	<0.01
Error	18,437	4,171.68	0.23		
Total	18,648	5,604.60	0.30		
Without interaction					
Model	31	1,100.02	35.48	147.83	<0.01
Year	19	908.42	47.81	199.21	<0.01
Qtr	3	107.36	35.79	149.11	<0.01
TC	9	84.24	9.36	39.00	<0.01
Error	18,617	4,504.58	0.24		
Total	18,648	5,604.60	0.30		
Southern New England					
With interaction					
Model	217	2,859.95	13.18	33.79	<0.01
Year	19	2,085.95	109.79	281.50	<0.01
Qtr	3	111.50	37.17	95.30	<0.01
TC	6	59.80	9.97	25.56	<0.01
Yr*Tc	114	257.12	2.26	5.78	<0.01
Yr*Qtr	57	304.89	5.35	13.72	<0.01
Qtr*Tc	18	40.69	2.26	5.80	<0.01
Error	26,879	10,612.21	0.39		
Total	27,096	13,472.16	0.50		
Without interaction					
Model	28	2,257.25	80.62	196.62	<0.01
Year	19	2,085.95	109.79	267.77	<0.01
Qtr	3	111.50	37.17	90.66	<0.01
TC	6	59.80	9.97	24.31	<0.01
Error	27,068	11,214.91	0.41		
Total	27,096	13,472.16	0.50		
Cape Cod					
With interaction					
Model	247	2,438.73	9.87	24.68	<0.01
Year	19	166.49	8.76	21.91	<0.01
Qtr	3	174.44	58.15	145.37	<0.01
TC	9	1,331.92	147.99	369.98	<0.01
Yr*Tc	135	526.18	3.90	9.74	<0.01
Yr*Qtr	57	167.62	2.94	7.35	<0.01
Qtr*Tc	24	72.09	3.00	7.51	<0.01
Error	19,097	7,731.24	0.40		
Total	19,344	10,169.97	0.53		
Without interaction					
Model	31	1,672.84	53.96	122.64	<0.01
Year	19	166.49	8.76	19.92	<0.01
Qtr	3	174.44	58.15	132.15	<0.01
TC	9	1,331.92	147.99	336.34	<0.01
Error	19,313	8,497.13	0.44		
Total	19,344	10,169.97	0.53		

TABLE 7.—Tonnage class, quarter, and year coefficients derived from a three-way linear model for the 1964–83 period for yellowtail flounder stocks on Georges Bank, Southern New England, and Cape Cod grounds.

	Georges Bank	Southern New England	Cape Cod
Tonnage class			
21	—	0.92	0.32
22	—	0.92	0.50
23	—	0.92	0.57
24	0.57	0.93	0.80
25	0.80	0.96	1.00
31	0.96	0.92	1.03
32	1.00	1.00	0.84
33	1.08	1.09	1.00
41	1.13	1.05	1.24
42	1.19	—	—
Quarter			
1	0.96	1.00	1.07
2	0.89	1.06	1.15
3	1.09	1.18	0.90
4	1.00	1.00	1.00
Year			
1964	1.00	1.00	1.00
1965	0.73	0.72	0.84
1966	0.55	0.54	0.84
1967	0.54	0.60	0.81
1968	0.68	0.79	0.93
1969	0.61	0.77	1.06
1970	0.58	0.75	1.00
1971	0.49	0.63	0.95
1972	0.45	0.65	0.88
1973	0.55	0.49	0.84
1974	0.42	0.45	0.77
1975	0.36	0.30	0.72
1976	0.37	0.25	0.76
1977	0.37	0.36	0.74
1978	0.34	0.39	0.83
1979	0.48	0.52	0.85
1980	0.55	0.56	0.78
1981	0.46	0.54	0.80
1982	0.44	0.71	0.77
1983	0.40	0.70	0.78

DISCUSSION

The analytical approach adopted in this paper is based on the hypothesis that CPUE of yellowtail flounder differs among the various tonnage classes of vessels and geographic regions associated with the fishery. In all of the analyses, the null hypothesis (i.e., no significant differences) was rejected only when the probability of obtaining a greater F statistic was <0.01. Even at this probability level, statistically significant results were often obtained when differences among variable levels appeared to be minimal due primarily to the large number of observations included in most analyses.

The initial series of ANOVAs, based on pooled CPUE data from all statistical areas encompass-

ing the three stocks, provided sufficient evidence to reject the null hypothesis. In each of the 20 years analyzed, the main effects of tonnage class and statistical area represented highly significant ($P < 0.01$) sources of variation. The tonnage class-area interaction term was also highly significant in all cases, implying that vessels of various tonnage classes exhibit different CPUE trends relative to each other in different areas.

The initial results established the basis for further investigations. In subsequent analyses, the data were grouped to test the null hypothesis that no significant differences in CPUE existed among the three traditionally accepted stock definitions (Georges Bank, Southern New England, and Cape Cod). The highly significant differences obtained in 19 out of 20 years indicate that catch rates differ among the three stocks. The resulting highly significant tonnage class-stock area interaction term obtained from the ANOVAs in all years suggests that standardization of CPUE among tonnage classes should be performed separately for each stock.

Analysis of variance within each stock provided the final basis for performing the standardized CPUE calculations. In these tests, the rejection of the null hypothesis for tonnage class main effects in all years for each stock suggests that separate fishing power coefficients must be calculated for each tonnage class even though the coefficients are similar in many cases. The ANOVA results also indicated that differences in CPUE among statistical areas within each stock were highly significant in 80% or more of the years implying that, within each stock region, yellowtail abundance is not homogeneous. This is not surprising since yellowtail flounder are prevalent only on certain grounds within each geographic region. Further analyses of the data by depth indicated no overall significant differences in CPUE between the two primary depth zones (1–55 m and 56–110 m) where yellowtail flounder are consistently caught.

The infrequent number of significant interactions on Georges Bank and Cape Cod grounds relative to Southern New England (Table 4) suggests a greater independence of the tonnage class and area main effects with respect to CPUE, i.e. both large and small vessels exhibited relatively similar changes in mean CPUE among statistical areas within each stock. In choosing data sets for computing fishing power coefficients we sought to minimize the amount of interaction among the vessel tonnage classes and geographic areas involved. This criterion was met to a greater extent for the Cape Cod and Georges Bank stocks than for the Southern New England stocks. It appears that yellowtail flounder inhabiting this region are subject to a more complex set of interactions perhaps due to temperature and bottom type. We decided, however, to accept the results for each of the three stocks and proceed with the calculations of fishing power coefficients.

Annual fishing power coefficients computed for each vessel tonnage class fishing on Georges Bank, Southern New England, and Cape Cod grounds provided a basis for examining the consistency in relative fishing power of individual tonnage classes over time. Annual deviations for Georges Bank and Southern New England grounds indicated a gradual change in relative fishing power of most tonnage classes between 1964 and 1983, and tests for autocorrelation of residuals indicated significant time effects. On these grounds, larger vessels exhibited higher catch rates relative to the standard in the later years as compared with the earlier years. Since many of the larger vessels have been replaced in recent years by newer vessels which are, presumably, equipped with more sophisticated electronics, any attempt to relate CPUE to stock abundance must account for such technological advances.

Similarly, changes in seasonal availability are often great enough to mask interannual variation in stock abundance. Thus, the presence of significant tonnage class-season interactions may be explained by the ability of certain vessel classes to effectively target seasonal concentrations. Since peak spawning of yellowtail flounder occurs during late spring (Lux 1964), the presence of high seasonal coefficients during the second and third quarters is not surprising.

By specifying the model to include tonnage class, annual, and seasonal components, we have attempted to account for technological and seasonal availability factors which interact with temporal changes in abundance. Although other factors could be incorporated in the model to account for a larger portion of the variation in CPUE, analyses of historical commercial fishing operations of this type are often limited to those attributes which can be directly linked to landings records (Kimura 1981; Westrheim and Foucher 1985). An alternate approach adopted by Stern and Hennemuth (1975) involved the use of a study fleet of selected vessels whose characteristics and fishing practices were closely monitored.

In our study, factors were selected for inclusion in the model based on prior knowledge of fleet characteristics and seasonal and spatial distribution patterns of the species. Despite this, the three attributes incorporated in the final model accounted for 15–25% of the total variation in CPUE, depending on the stock. Undoubtedly, other factors such as experience of the captain, net design and rigging, and variation in local fish abundance contribute substantially to overall variation in catch rates.

Differences between the annual CPUE estimates based on Lux's original fishing power coefficients and the recalculated indices occur in many cases because of shifts in the vessel composition of the fleet over the past 20 years. The inclusion of larger vessels in the more recent years, particularly on Georges Bank and Southern New England grounds, may account for the consistently higher CPUE estimates obtained for these areas since the mid-1970's. On Cape Cod grounds, CPUE estimates differ substantially prior to this time. Lux (1964) has stated that a relatively low proportion of the landings from this area were used in his CPUE computations and, consequently, the indices were not considered to be as valid a measure of relative abundance as those obtained for Georges Bank and Southern New England. Our analyses for Cape Cod grounds, based on data for the period since 1964, are subject to the same concerns since a large proportion of the yellowtail flounder landings continues to be taken incidentally.

Although the revised standardized CPUE estimates presented in this paper are based on a different standardization technique, trends are generally similar to those obtained previously. The revised procedure, however, accounts for seasonal and technological influences and insures complete representation of all vessel classes engaged in the yellowtail fishery.

ACKNOWLEDGMENTS

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REDUCING THE BYCATCH IN A COMMERCIAL TROTLINE FISHERY

LAWRENCE W. MCEACHRON,[1] JEFF F. DOERZBACHER,[2] GARY C. MATLOCK,[2]
ALBERT W. GREEN,[2] AND GARY E. SAUL[2]

ABSTRACT

Reducing the bycatch of red drum, *Sciaenops ocellatus*, and spotted seatrout, *Cynoscion nebulosus*, in the Texas commercial trotline fishery is desirable. Hook placement within the water column was examined as a means of accomplishing this objective. The commercial trotline fishery was simulated in the Laguna Madre during February 1985 through January 1986. Requiring placement of trotline hooks on bottom will reduce bycatch of red drum, spotted seatrout, and other nonmarketable fishes and improve operational efficiency of commercial fishermen without significantly reducing catch of black drum, *Pogonias cromis*, a target commercial species. Other than crab and shrimp being more effective baits than oleander leaves, no other generalization could be made concerning baits and seasons.

Longlines catch species unwanted or legally nonretainable by fishermen and have been regulated to reduce the bycatch of nontargeted species (South Atlantic Fishery Management Council 1985). Trotlines (Figs. 1, 2) are a specialized longline used in shallow (<4 m) Texas estuaries to catch fish (Simmons and Breuer 1962; Breuer 1973, 1974, 1975; Matlock 1980). Red drum, *Sciaenops ocellatus*, and spotted seatrout, *Cynoscion nebulosus*, were the primary targets until 1981 when their sale was prohibited because of overfishing (Matlock et al. 1979; Anonymous 1979, 1981, 1983). The effort has since been redirected toward black drum, *Pogonias cromis*. Regulations requiring the use of circle hooks and placement of the mainline under water were enacted to reduce the bycatch of red drum and spotted seatrout. However, a bycatch still occurs. This study was conducted to determine if the bycatch could be further reduced by additional regulation of where in the water column hooks are fished and bait types.

MATERIALS AND METHODS

The catch on trotlines with hooks placed on the bottom or in the top of the water column was compared by simulating commercial fishing techniques in the Laguna Madre, TX (Fig. 3). Bottom trotlines were set with the mainline on the bottom. Top trotlines had the mainline floated with the hooks suspended in water ≥0.6 m deep to insure hooks fished in the water column. Texas Parks and Wildlife Department (TPWD) trotlines were set in the same area as commercial trotlines. Commercial fishermen were contacted by telephone within 24 hours prior to TPWD sets to determine areas of commercial activity. All TPWD trotlines were at least 15 m apart.

Trotlines with 100 hooks each were built according to commercial fishermen specifications (McEachron et al. 1985). The mainline (182.9 m long) consisted of #36 nylon twine, knotted twice every 1.8 m for swivel (1/0 black brass barrel) placement (Figs. 1, 2). Hooks (#8 Mustad 39960ST) were attached by a 610–686 mm long staging (56.7 kg test monofiliament) to the swivel at 1.8 m intervals. Stakes (51 cm × 76 mm) and/or anchors were placed on each end to stretch the mainline. Floats (3.8 L) were attached to the mainline every 15 hooks for navigation identification.

Eighteen trotlines were set overnight each month in both the upper and lower Laguna Madre during 1 February 1985 through 31 January 1986. Six (3 top; 3 bottom) were set during each of two monthly sampling periods (first and last 15 days of the month). Another six sets were made in either the first or last half of each month; the period was randomly selected each month. Each trotline was baited completely with one of three bait types—cut portions of blue crab, *Callinectes sapidus*; dead shrimp, *Penaeus* sp.; or oleander, *Nerium* sp. leaves—so that all bait types were used on both top and bottom trotlines during every period. These baits represented the most

[1]Texas Parks and Wildlife Department, P.O. Box 1717, Rockport, TX 78382.
[2]Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, TX 78744.

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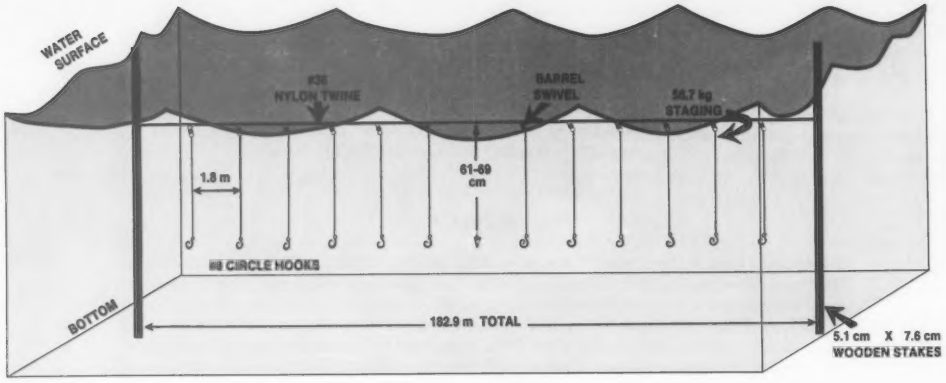

FIGURE 1.—Top trotline.

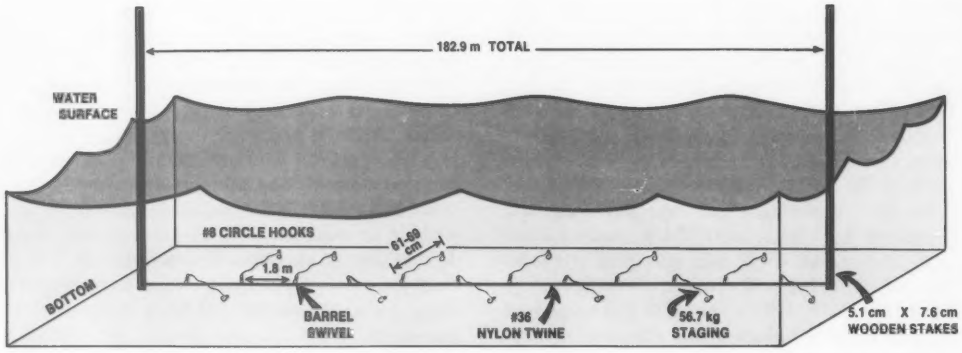

FIGURE 2.—Bottom trotline.

commonly used baits by commercial trotline fishermen (McEachron et al. 1980, 1986).

Fishes caught were identified (Hoese and Moore 1977; Robins et al. 1980), counted (Table 1), and total length (TL) was measured to the nearest 1 mm. Data were pooled into fall (September–November), winter (December–February), spring (March–May), and summer (June–August) to examine seasonal variation.

A catch rate (No./line · h) for black drum; red drum; spotted seatrout; hardhead catfish *Arius felis*; and total fishes was computed for each trotline set by dividing the number caught by the number of hours fished. Catch rates were transformed to log (catch rate + 1) and analyzed using a four-factor fixed-effects model analysis of variance (AOV). The four factors were 1) hook placement, at two levels—top and bottom; 2) bait, at three levels—crab, shimp, and leaves; 3) bay, at two levels—upper Laguna Madre and lower Laguna Madre; 4) season, at four levels—fall, winter, spring, and summer.

Differences in main effect means were evaluated with Ducan's multiple range test. However, when significant first-order interactions were found, comparisons were made within levels of the interacting factors using the mean square error (MSE) from the AOV.

Total lengths of each species were analyzed in a nested AOV to investigate differences among the four factors. However, because fish were not caught in all factor level combinations, factors and/or factor levels for each species were eliminated from analyses. Spotted seatrout lengths

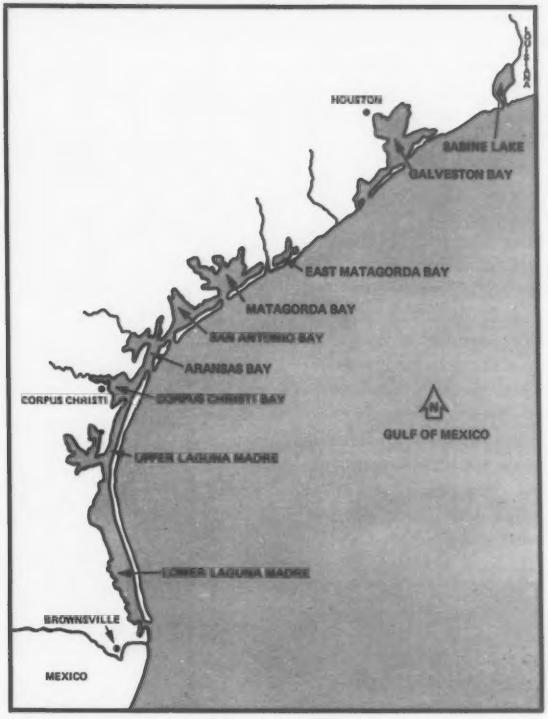

FIGURE 3.—Texas coast.

TABLE 1.—Number of fishes caught on trotlines in the upper and lower Laguna Madre during February 1985-January 1986.

Species	Upper Laguna Madre	Lower Laguna Madre	Total
Arius felis	977	1,652	2,629
Sciaenops ocellatus	352	658	1,010
Pogonias cromis	67	265	332
Cynoscion nebulosus	29	103	132
Micropogonias undulatus	36	51	87
Opsanus beta	34	1	35
Archosargus probatocephalus	1	24	25
Dasyatis americana	0	17	17
Dasyatis sabina	6	7	13
Elops saurus	4	4	8
Orthopristis chrysoptera	1	7	8
Bagre marinus	1	4	5
Lagodon rhomboides	0	5	5
Paralichthys lethostigma	1	3	4
Rhinoptera bonasus	0	4	4
Chilomycterus schoepfi	0	3	3
Ophichthus gomesi	3	0	3
Cynoscion arenarius	0	2	2
Negaprion brevirostris	0	1	1
Trachinotus carolinus	0	1	1
All species	1,512	2,812	4,324

were pooled for both bay systems because an insufficient number of spotted seatrout were caught for individual bay analyses. Factor levels eliminated from length analyses were leaves and winter from hardhead catfish, leaves and crab from spotted seatrout, and fall, spring, and summer from black drum. Spring and winter red drum lengths were pooled. Lower Laguna Madre data only were used for red drum, black drum, and hardhead catfish length analyses. Each measured fish length was an observational unit of a trotline set. Sets were a random factor nested within fixed main effect combinations. The nested set effect mean square was used for testing other effects when the set effect was significant. However, the AOV yields approximate F values because unequal numbers of fish were caught among sets.

SAS procedures (SAS Institute, Inc. 1980, 1982) were used for all analyses. The significance level for each AOV test was $\alpha = 0.01$ because the AOV used to examine catch rates of each species had 15 potential F tests. This alpha value assured that

the family level of significance would not exceed 0.15. All other tests were made with a significance level of $\alpha = 0.05$. Mean catch rates and confidence intervals computed from transformed data were back-transformed for tabular and graphic presentation (Elliott 1979).

RESULTS

Fishing trotlines on the bottom reduces bycatch without affecting catches of black drum, the target species. A significant difference could not be detected between black drum catch rates on top and bottom trotlines regardless of bait, season, or bay (Tables 2, 3). Catch rates for hardhead catfish, red drum, spotted seatrout and total fishes were significantly lower on bottom trotlines than on top trotlines (Tables 2, 3). Differences in catch rates between top and bottom trotlines for hardhead catfish, red drum, and total fishes did not vary significantly among seasons and baits but did vary between bays based on the first-order interactions (Tables 4, 5). A significant second-order interaction of position × bay × bait for spotted seatrout revealed that differences between top and bottom trotlines were affected by both bait and bay but not by season (Fig. 4).

No significant difference was found in red drum catch rates among baits nor in spotted seatrout catch rates among seasons (Tables 2, 3). All other main effects were significant for catch rates of all species and total fishes. Of the possible first-order interactions involving bait, season, and bay, only season × bait for hardhead catfish, red drum, and total fishes, bait × bay for black drum and total fishes, and season × bay for black drum, hardhead catfish, and total fishes were significant (Tables 4, 5). The second-order interaction of bait × bay × season for total fishes was significant (Fig. 5).

No significant differences were found in mean lengths of black drum, hardhead catfish, red drum, and spotted seatrout between top and bottom trotlines (Tables 6–8). Significant differences in mean length of hardhead catfish were detected for main effects of bait and season (Table 7).

DISCUSSION

Management objectives could be better met by requiring placement of trotline hooks on bottom than by allowing hooks to be fished from the surface. Red drum and spotted seatrout mortality would be reduced without significantly affecting

TABLE 2.—Mean back-transformed catch rate (No./line · h) and associated 95% confidence interval of black drum, hardhead catfish, red drum, spotted seatrout, and total fish caught on top and bottom trotlines by bait, bay, and season during February 1985-January 1986. Numbers in parentheses are the lower and upper values for the 95% confidence interval.

Species	Position[1]		Bait[2]			Bay[1]		Season[3]			
	Top	Bottom	Crab	Shrimp	Leaves	Upper Laguna Madre	Lower Laguna Madre	Fall	Winter	Spring	Summer
Black drum	0.049 (0.033-0.066)	0.039 (0.025-0.053)	0.072 (0.046-0.099)	0.044 (0.027-0.061)	0.017 (0.007-0.027)	0.017 (0.010-0.024)	0.071 (0.051-0.092)	0.019 (0.010-0.028)	0.113 (0.073-0.153)	0.037 (0.021-0.052)	0.010 (0.004-0.016)
Hardhead catfish	0.486 (0.411-0.566)	0.207 (0.165-0.249)	0.674 (0.563-0.793)	0.288 (0.233-0.345)	0.090 (0.055-0.126)	0.265 (0.216-0.316)	0.424 (0.355-0.498)	0.312 (0.246-0.381)	0.213 (0.136-0.295)	0.530 (0.418-0.651)	0.326 (0.250-0.407)
Red drum	0.209 (0.167-0.253)	0.047 (0.031-0.062)	0.123 (0.087-0.162)	0.155 (0.112-0.199)	0.103 (0.064-0.140)	0.089 (0.067-0.114)	0.166 (0.129-0.204)	0.072 (0.048-0.096)	0.299 (0.215-0.388)	0.062 (0.041-0.084)	0.084 (0.057-0.112)
Spotted seatrout	0.031 (0.022-0.041)	0.005 (0.001-0.009)	0.007 (0.003-0.011)	0.037 (0.023-0.051)	0.010 (0.004-0.016)	0.008 (0.003-0.012)	0.028 (0.019-0.038)	0.014 (0.007-0.022)	0.028 (0.014-0.042)	0.009 (0.004-0.015)	0.020 (0.008-0.033)
Total fish	0.839 (0.739-0.945)	0.319 (0.268-0.372)	0.925 (0.795-1.064)	0.578 (0.493-0.667)	0.234 (0.176-0.295)	0.408 (0.346-0.472)	0.745 (0.649-0.846)	0.452 (0.370-0.540)	0.717 (0.571-0.876)	0.677 (0.553-0.811)	0.460 (0.367-0.559)

[1] N = 216 for each species.
[2] N = 144 for each species.
[3] N = 108 for each species.

TABLE 3.—Summary of results of four-way AOV's of the mean transformed catch ra

Source of variation	df	Black drum			Red dru	
		Sum of squares	*F*	*PR* > *F*	Sum of squares	*F*
Total	431	0.9803			3.5951	
Position	1	0.0015	0.82	0.37	0.2736	43.12
Bait	2	0.0252	6.90	<0.01	0.0217	1.71
Season	3	0.0789	14.41	<0.01	0.2932	15.41
Bay system	1	0.0380	20.81	<0.01	0.0611	9.63
Position × bait	2	0.0005	0.13	0.88	0.0091	0.72
Position × season	3	0.0008	0.15	0.93	0.0664	3.49
Position × bay systems	1	0.0006	0.33	0.57	0.0430	6.77
Bait × bay systems	2	0.0265	7.27	<0.01	0.0434	3.42
Bait × season	6	0.0179	1.63	0.14	0.2014	5.29
Bay systems × season	3	0.0588	10.74	<0.01	0.0045	0.23
Position × bait × bay systems	2	0.0004	0.13	0.87	0.0152	1.20
Position × bait × season	6	0.0018	0.16	0.99	0.0078	0.20
Position × bay systems × season	3	0.0003	0.06	0.98	0.0153	0.80
Bait × bay systems × season	6	0.0264	2.41	0.03	0.0806	2.12
Position × bait × bay systems × season	6	0.0013	0.12	0.99	0.0227	0.60
Error	384	0.7012			2.4363	

TABLE 4.—Mean transformed catch rate of position
Means followed by the same letter in a row under a

Bay system	Position × Hardhead catfish		
	Top	Bottom	
Upper Laguna Madre	0.315 A	0.216 A	(
Lower Laguna Madre	0.665 A	0.197 B	(

TABLE 5.—Mean transformed catch rate of season × ba
followed by the same letter in a row under a species hea
Laguna Madre; LLM = Lower Laguna Madre.

Season	Season × bait				
	Hardhead catfish			R	
	Crab	Shrimp	Leaves	Crab	
Fall	0.614 A	0.310 B	0.212 C	0.100 A	(
Winter	0.329 A	0.200 A	0.119 A	0.224 A	(
Spring	1.006 A	0.444 B	0.178 C	0.076 A	(
Summer	0.757 A	0.201 B	0.045 C	0.100 A	(

atch rate on top and bottom trotlines in the Laguna Madre during February 1985-January 1986.

Red drum		Spotted seatrout			Hardhead catfish			Total		
F	*PR* > *F*	Sum of squares	*F*	*PR* > *F*	Sum of squares	*F*	*PR* > *F*	Sum of squares	*F*	*PR* > *F*
		0.2369			9.4078			12.3038		
43.12	<0.01	0.0115	25.88	<0.01	0.5652	41.23	<0.01	1.7030	121.71	<0.01
1.71	0.18	0.0113	12.68	<0.01	1.7919	65.36	<0.01	2.1632	77.30	<0.01
15.41	<0.01	0.0028	2.11	0.10	0.4590	11.16	<0.01	0.2515	5.99	<0.01
9.63	<0.01	0.0070	15.67	<0.01	0.1716	12.51	<0.01	0.6792	48.54	<0.01
0.72	0.49	0.0026	2.89	0.06	0.0380	1.39	0.25	0.0149	0.53	0.59
3.49	0.02	0.0010	0.77	0.51	0.0393	0.96	0.41	0.0326	0.78	0.51
6.77	0.01	0.0118	26.60	<0.01	0.2229	16.26	<0.01	0.5231	37.38	<0.01
3.42	0.03	0.0012	1.40	0.25	0.0135	0.49	0.61	0.1366	4.88	0.01
5.29	<0.01	0.0050	1.86	0.09	0.3355	4.08	<0.01	0.4950	5.90	<0.01
0.23	0.87	0.0011	0.82	0.48	0.2675	6.50	<0.01	0.4854	11.56	<0.01
1.20	0.30	0.0050	5.66	<0.01	0.0026	0.10	0.91	0.0006	0.02	0.98
0.20	0.98	0.0008	0.30	0.94	0.0499	0.61	0.72	0.0390	0.46	0.83
0.80	0.49	0.0011	0.83	0.48	0.0720	1.75	0.16	0.0904	2.15	0.09
2.12	0.05	0.0009	0.34	0.91	0.0761	0.93	0.48	0.2381	2.84	0.01
0.60	0.73	0.0026	0.96	0.45	0.0384	0.47	0.83	0.0781	0.93	0.47
		0.1711			5.2641			5.3731		

osition × bay and bait × bay in significant two-way interactions.
nder a species heading are not significantly ($P > 0.05$) different.

sition × bay			Bait × bay		
	Red drum		Black drum		
m	Top	Bottom	Crab	Shrimp	Leaves
A	0.135 A	0.044 B	0.012 A	0.036 A	0.003 A
B	0.286 A	0.050 B	0.133 A	0.052 B	0.031 B

n × bait and season × bay in significant two-way interactions. Means
cies heading are not significantly ($P > 0.05$) different. ULM = upper

it			Season × bay			
Red drum			Black drum		Hardhead catfish	
ab	Shrimp	Leaves	ULM	LLM	ULM	LLM
0 A	0.068 A	0.047 A	0.008 A	0.030 A	0.326 A	0.298 A
4 A	0.494 B	0.183 B	0.023 A	0.205 B	0.001 A	0.444 B
6 A	0.035 A	0.077 A	0.038 A	0.035 A	0.445 A	0.617 B
0 A	0.044 A	0.109 A	0.000 A	0.019 A	0.305 A	0.349 A

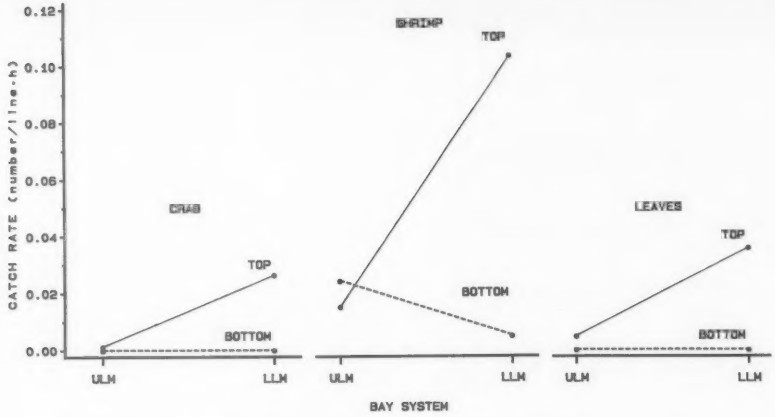

FIGURE 4.—Significant second-order interaction among positions, baits, and bay system for spotted seatrout catch rates. LLM = lower Laguna Madre, ULM = upper Laguna Madre.

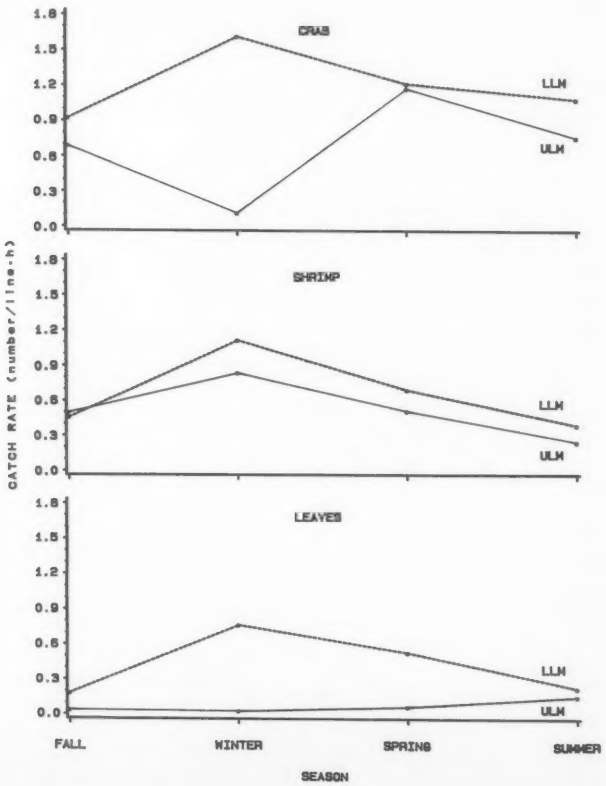

FIGURE 5.—Significant second-order interaction among bait types, bay system, and seasons for total fishes catch rates. LLM = lower Laguna Madre, ULM = upper Laguna Madre.

TABLE 6.—Mean length (mm ± 1SE) of black drum, hardhead catfish, red drum, and spotted seatrout caught on top and bottom trotlines by bait, bay and season during February 1985–January 1986. Number in parentheses is number of fish measured.

Species	Position		Bait		
	Top	Bottom	Crab	Shrimp	Leaves
Black drum	539 ± 10 (177)	550 ± 13 (146)	566 ± 11 (172)	493 ± 12 (108)	588 ± 21 (43)
Hardhead catfish	338 ± 1 (1,363)	343 ± 2 (675)	346 ± 1 (1,201)	328 ± 2 (651)	337 ± 3 (186)
Red drum	521 ± 4 (657)	504 ± 9 (173)	540 ± 6 (260)	481 ± 6 (336)	542 ± 7 (234)
Spotted seatrout	439 ± 9 (111)	420 ± 24 (18)	471 ± 23 (17)	426 ± 10 (86)	445 ± 19 (26)

Species	Bay		Season			
	Upper Laguna Madre	Lower Laguna Madre	Fall	Winter	Spring	Summer
Black drum	484 ± 19 (67)	560 ± 8 (256)	464 ± 20 (35)	538 ± 8 (201)	630 ± 21 (71)	416 ± 19 (16)
Hardhead catfish	327 ± 1 (824)	348 ± 1 (1,214)	329 ± 2 (538)	368 ± 2 (277)	333 ± 2 (724)	345 ± 2 (499)
Red drum	506 ± 7 (308)	523 ± 5 (522)	493 ± 11 (133)	506 ± 5 (427)	546 ± 9 (114)	551 ± 10 (146)
Spotted seatrout	411 ± 15 (29)	443 ± 10 (100)	410 ± 21 (25)	404 ± 12 (51)	482 ± 25 (16)	478 ± 13 (37)

TABLE 7.—Summary of results of the AOV's of mean length for black drum (winter season only), hardhead catfish (excludes leaves and winter season), and red drum (winter and spring seasons combined) on top and bottom trotlines in lower Laguna Madre during February 1985–January 1986. NA = not analyzed.

Source of variation	Black drum				Hardhead catfish				Red drum			
	df	Sum of squares	*F*	*PR* > *F*	df	Sum of squares	*F*	*PR* > *F*	df	Sum of squares	*F*	*PR* > *F*
Total	176	1,941,401			1,050	2,310,898			521	6,484,793		
Position	1	5,978	0.15	0.70	1	80	0.02	0.90	1	6,122	0.26	0.61
Bait	2	15,082	0.19	0.83	1	33,650	6.60	0.01	2	89,151	1.90	0.15
Season	NA				3	89,202	5.83	<0.01	2	133,190	2.85	0.06
Position × bait	2	49,063	0.69	0.55	1	8,242	1.62	0.21	2	10,913	0.23	0.79
Season × position	NA				3	1,517	0.10	0.96	2	789	0.02	0.98
Season × bait	NA				3	6,132	0.40	0.75	4	68,535	0.73	0.57
Season × position × bait	NA				3	10,269	0.67	0.57	4	63,388	0.68	0.61
Set (position × bait)	27	10,906,616	8.26	<0.01	NA				NA			
Set (season × position × bait)	NA				89	453,750	3.22	<0.01	91	2,129,491	2.61	<0.01
Error	144	704,611			946	1,499,474			413	3,706,235		

TABLE 8.—Summary of results of the AOV of mean length for spotted seatrout (shrimp bait only) on top and bottom trotlines in upper and lower Laguna Madre combined during February 1985–January 1986.

Source of variation	df	Sum of squares	*F*	*PR*>*F*
Total	85	750,362		
Position	1	601	0.04	0.84
Season	3	58,796	1.32	0.29
Position × season	3	58,462	1.31	0.29
Set (position × season)	28	416,855	3.42	<0.01
Error	50	217,744		

black drum catches. Operational efficiency of commercial fishermen should improve with less handling of nontarget species. Mortality of nontarget fishes would decrease because they would not be caught and subsequently handled. For red drum and spotted seatrout that are caught, survival would be high for those released back into the water. Survival of released red drum caught on trotlines in winter and summer and of spotted seatrout in winter was 100% (Martin et al. 1987). About 50% of the spotted seatrout died in summer cage studies; but few commercial trotlines are fished during this period (TPWD unpubl. data). Thus, the goal of reducing the catch of nontarget species and reducing mortality due to trotlines can be achieved with minimal impact on the commercial fishermen.

Interactions between bay system and the other three factors for some species probably reflect differences in relative abundance. Fewer fish were available to be caught in upper Laguna Madre than in lower Laguna Madre (Crowe et al. 1986). The effects of bait and season on trotline catches cannot be determined in bay systems where the fish abundance approaches zero.

No spotted seatrout were caught on crab bait on bottom in either bay; but they were caught on all baits on top in the lower Laguna Madre leading to the significant second-order interaction of position × bay × bait. This condition was not unexpected because spotted seatrout are predominately sight feeders (Vetter 1977), and might not take baits on bottom as readily as baits suspended in the water column.

Crab and shrimp were more effective baits than oleander leaves for all four species. No other generalizations could be made concerning baits and seasons. Selection of crab or shrimp as the bait of choice for reducing bycatch while maximizing black drum catch is unclear because catch rates for black drum and red drum were greater on crab than shrimp, especially in winter.

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LARVAL DEVELOPMENT OF BLUE GRENADIER, *MACRURONUS NOVAEZELANDIAE* (HECTOR), IN TASMANIAN WATERS

B. D. BRUCE[1]

ABSTRACT

The development of *Macruronus novaezelandiae* is described and illustrated from both reared specimens and larvae from Tasmanian waters. Eggs of *M. novaezelandiae* are pelagic, spherical (1.08–1.18 mm diameter), and have a single oil droplet (0.36–0.42 mm diameter). Eggs hatch after 55–60 hours at 14°–19°C. Larvae are 2.2–2.3 mm at hatching. Characteristic pigmentation, a myomere count of 78–80, and the sequence of fin development separate *M. novaezelandiae* from other known gadiform larvae. Development is direct, with no marked change in body morphology. Fin development proceeds in the sequence: second dorsal, anal, first dorsal, pelvic, caudal, pectoral. However, adult fin complements are reached in the sequence: first dorsal, pelvic, anal, second dorsal, caudal, pectoral.

Caudal development is late in *Macruronus*. Flexion begins at 20 mm and is not complete until 28 mm. The caudal fin is based on two ural centra, four hypurals, two epurals, and a parhypural. X and Y bones are present although they are not readily distinguishable from dorsal and anal pterygiophores.

The genus *Macruronus* comprises four nominal species, which occur in southern temperate continental shelf and slope regions. Two species, *Macruronus novaezelandiae* and *M. magellanicus* support commercial fisheries. The blue grenadier, *M. novaezelandiae*, forms the basis of fisheries in New Zealand and Australia where total annual catches range up to 97,750 and 1,100 t respectively (Patchell 1982; Wilson 1981, 1982). *Macruronus magellanicus* is fished commercially off South America. The remaining species, *M. maderensis* and *M. capensis*, are known only from a limited number of specimens (Svetovidov 1948; Cohen 1986). Despite their economic importance and widespread distribution, very little is known of the early life history of any member of the genus. Patchell (1982) identified winter spawning grounds on the west coast of the South Island for New Zealand populations of *M. novaezelandiae* and similarly Wilson (1981, 1982) has suggested a winter spawning, on the west coast of Tasmania, for Australian *M. novaezelandiae*. This paper presents the first published information on the larvae of *Macruronus*.

In 1984, the Division of Fisheries Research of the Commonwealth Scientific and Industrial Research Organization established a multidisciplinary program to investigate the biology and ecology of blue grenadier in Tasmanian waters. An integral part of this program was a study of larval ecology. As such, it was first necessary to establish criteria for the identification of blue grenadier larvae. This paper describes the larval development of *M. novaezealandiae* from Tasmanian waters.

MATERIALS AND METHODS

Specimens were obtained from samples collected aboard the CSIRO Fisheries Research Vessel *Soela* between April 1984 and September 1985. Details of sampling strategies, locations, and procedures will be described in a subsequent manuscript. Larvae were obtained by sampling with a rectangular midwater trawl (RMT 1+8; Baker et al. 1973), a 1 m diameter ring net (500 μm mesh), and free-fall, vertical drop nets of 64 μm and 200 μm mesh (Heron 1982). Juvenile specimens were obtained with an Engels 352 pelagic trawl fitted with a 10 mm liner.

Newly hatched larvae were reared from eggs stripped and fertilized at sea. Eggs and milt stripped from ripe adults trawled from 500 m were mixed in 1 L plastic jars filled with seawater. Despite the jars being located in a seawater bath, incubation temperatures varied considerably (14°–19°C). On return to the laboratories at Hobart, the eggs were transferred to 2 L glass jars and placed in a constant temper-

[1]CSIRO Division of Fisheries Research, GPO Box 1538, Hobart, Tasmania 7001, Australia; present address: South Australia Department of Fisheries, GPO Box 1625, Adelaide, South Australia 5001, Australia.

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ature incubation chamber set at 14.0° ± 0.2°C. Incubation jars were not aerated, and no attempt was made to feed the larvae.

All specimens used for description were fixed in a 10% formalin-seawater solution buffered with sodium β-glycerophosphate and later transferred to a 5% solution.

This description is based on a series of 74 larvae, 2.2–34.2 mm in length, although comments on pigment and meristic variability stem from routine examination of several hundred specimens. A representative series of larvae is deposited with the South Australian Museum, Adelaide, South Australia.

Developmental terminology follows Ahlstrom et al. (1976). Body measurements follow Matarese et al. (1981). Length measurements are reported as notochord length, NL (i.e., from the snout tip to the end of the notochord) in preflexion and flexion larvae, and standard length, SL (i.e., from the snout tip to the posterior margin of the superior hypural elements) in postflexion larvae and juveniles. Larvae were measured under a dissecting microscope fitted with an ocular micrometer and a camera lucida. Juveniles were measured with vernier calipers.

Meristic counts and examination of ossification sequences were made on specimens cleared and stained using Alizarin Red S-KOH-glycerine (Hollister 1934). Caudal osteology follows Inada (1981), Marshall and Cohen (1973), and Monod (1968).

Vertebral counts include the first vertebrae, the neural spine of which is fused to the supraoccipital crest (Marshall 1966), and both ural centra. Vertebral centra were counted as ossified only when a complete band of stain connected both neural and haemal spines.

RESULTS

Identification of *M. novaezelandiae* larvae was based on their typical gadiform morphology (large head, compact gut, tapering body form), myomere count, and the development of confluent dorsal-caudal-anal fins (see section on Distinguishing Features). Identification of field-collected specimens was confirmed by comparison with reared larvae.

Distinguishing Features

Prior to median fin development, myomere counts are useful in separating *M. novaezelandiae* larvae (78–80) from similarly pigmented morid (41–72), macrourid (10–16 + 70 > 100), gadid (39–64) and other known merlucciid larvae (48–58) which they superficially resemble (Marshall and Iwamoto 1973; Fahay and Markle 1984; present study).

Both *M. novaezelandiae* and most morid larvae show moderately pedunculate pectoral fins, a feature common in gadiform larvae with delayed caudal development (Fahay and Markle 1984). Macrourid larvae, in contrast, have very prominently stalked pectorals and can further be separated from *M. novaezealandiae* and most morids by precocious development of the pelvic fin.

Size at caudal flexion and the sequence of fin development are also useful in separating *M. novaezelandiae* from all *Merluccius* species. In *Merluccius*, notochord flexion generally begins at about 9 mm and the caudal fin is the first to form (Dunn and Matarese 1984; Fahay and Markle 1984). *Macruronus novaezelandiae* larvae do not begin caudal flexion until approximately 20 mm, and the caudal fin is the second last to form.

Macruronus novaezelandiae larvae have 1–3 prominent melanophores along the ventral midline of the tail (although variable in appearance, see section on Trunk and Tail Pigmentation) and a double series of dorsal melanophores. When expanded, melanophores in these two regions coalesce to give the appearance of a broad postanal band. Postanal banding patterns are widespread in gadoid larvae (Fahay and Markle 1984); however, unlike many gadoid larvae, *M. novaezelandiae* lacks pigment at the notochord tip.

At larger sizes *M. novaezelandiae* larvae develop long-based dorsal and anal fins confluent with the caudal fin. Other gadoid larvae with this configuration have markedly different pigmentation (see Fahay and Markle 1984 for details). Ophidiiform larvae have confluent dorsal, caudal, and anal fins but can be separated from *M. novaezelandiae* by their lack of a separate first dorsal fin and general lack of body pigment (see Gordon et al. 1984).

Development

Embryonic development has not been treated in detail here as it is the subject of a manuscript in preparation by G. Patchell (Fisheries Research Centre, Wellington, New Zealand).

The pelagic eggs of blue grenadier are spherical, with an unsegmented yolk and a smooth cho-

rion. Late-stage eggs are 1.08–1.18 mm in diameter with a single oil droplet of 0.36–0.42 mm diameter (Fig. 1A). Reared larvae hatch at 2.2–2.3 mm after 55–60 hours (14°–19°C). Newly hatched larvae have a posteriorly positioned oil droplet and adopt a head down position in rearing containers. Yolk absorption was incomplete in specimens reared to 3.7 mm (6 days posthatch), although the smallest field-collected larvae (3.6 mm) had already completed yolk absorption. The anus opened laterally to the right in all reared larvae and 95% of field-collected larvae. The anus becomes symmetrical by 5.1 mm. A lateral anal opening in *M. novaezelandiae* is consistent with the developmental pattern reported for other gadiform species (Marak 1967; Matarese et al. 1981; Fahay and Markle 1984; Dunn and Vinter 1984).

Field-collected larvae are moderately elongate with the greatest body depth (16–22% body length) occurring at or near the pectoral fin base (Table 1). Head length as a proportion of body length (BL) remains relatively constant at about 22% BL throughout the larval phase, decreasing to about 17% BL in juveniles. Eye diameter decreases from 9% BL in preflexion larvae to 4% BL in juveniles. Depth at anus remains relatively constant at about 13% BL in larvae and juveniles. Distances from the snout tip to the first dorsal fin and from the snout tip to the anal fin decrease slightly during development from about 27% BL to 21% BL and 51% BL to 46% BL respectively.

Pigmentation

Although pigmentation in *M. novaezelandiae* is variable, certain features persist that, when combined with meristic and morphometric information, enable identification. Variation in the appearance of pigmentation is a result of differences in the number of melanophores and their degree of expansion. Although Badcock and Merrett (1976) suggested the appearance of melanophores can change on a diurnal rhythm, in the blue grenadier larvae examined, there was no conspicuous relationship between time caught and melanophore expansion.

Head Pigmentation

Newly hatched larvae (2.2–2.3 mm) have melanophores concentrated in front and behind the eye (Fig. 1B). Melanophores increase in number and extend over the sides of the head and snout by 3.3–3.5 mm (reared larvae, Fig. 1C). Melanophores migrate dorsally to the top of the head by 3.6 mm (Fig. 1D). Eyes become pigmented at this size in reared larvae. By 4.5 mm, the dorsal pigment on the head consists of a group of 3–11 melanophores scattered over the hindbrain and posteriorly to above the cleithrum. Pigment gradually extends over the midbrain, with 1 or 2 melanophores usually present between the eyes by 5.3 mm. Melanophores develop externally over these initial mid- and hindbrain spots and extend posteriorly as a double row to the dorsal fin anlage by 7.2 mm. Dorsal pigment gradually intensifies: melanophores increase in number and form a cap over mid- and hindbrains by 16.0 mm. Melanophores extend down between the eyes to the tip of the maxilla by 12.0 mm. Internal pigment expands over the forebrain in larvae from 9.0 to 15.0 mm.

Ventral pigment on the head first develops in 4.2 mm larvae as 3–5 melanophores between the dentaries. The number of melanophores increases to 10–12 by 12.0 mm.

TABLE 1.—Body proportions of larvae and juveniles of *Macruronus novaezelandiae* (expressed as percentage NL or SL): mean, standard deviation, range.

Body proportions	Preflexion 42			Flexion 4			Postflexion 4			Juvenile 2		
sample size	*X*	SD	range	*X*	SD	range	*X*	SD	range	*X*	SD	range
length (mm)	8.9	4.5	(3.6–19.0)	23.5	2.3	(20.6–26.1)	30.0	2.9	(27.6–34.2)	189.0	1.4	(188.0–190.0)
head length	22.7	1.7	(18.3–24.7)	23.7	1.0	(22.3–24.7)	22.3	1.4	(20.5–23.6)	17.6	0.4	(17.3–17.9)
eye diameter	9.2	0.7	(8.1–10.3)	7.9	0.4	(7.3–8.3)	7.3	0.7	(6.5–8.0)	4.2	0.4	(4.4–5.2)
snout length	6.1	0.9	(4.6–7.7)	6.2	0.6	(5.7–7.0)	5.9	0.5	(5.4–6.5)	4.9	0.1	(4.8–5.0)
depth at pectoral	22.3	1.7	(21.0–24.4)	17.9	0.6	(17.2–18.5)	16.6	2.0	(13.7–18.5)	13.1	0.1	(13.0–13.2)
depth at anus	12.0	2.4	(8.2–15.2)	13.1	0.3	(12.6–13.4)	13.0	0.8	(12.3–13.8)	12.7	0.6	(12.3–13.1)
snout to first dorsal fin	27.5	1.3	(25.2–29.3)	26.6	0.8	(26.0–27.7)	25.3	0.8	(24.2–26.0)	20.7	0.2	(20.6–20.9)
snout to anal fin	51.4	0.9	(50.0–52.6)	50.4	0.5	(49.6–50.6)	46.6	1.5	(45.0–48.4)	46.5	1.2	(45.7–47.4)

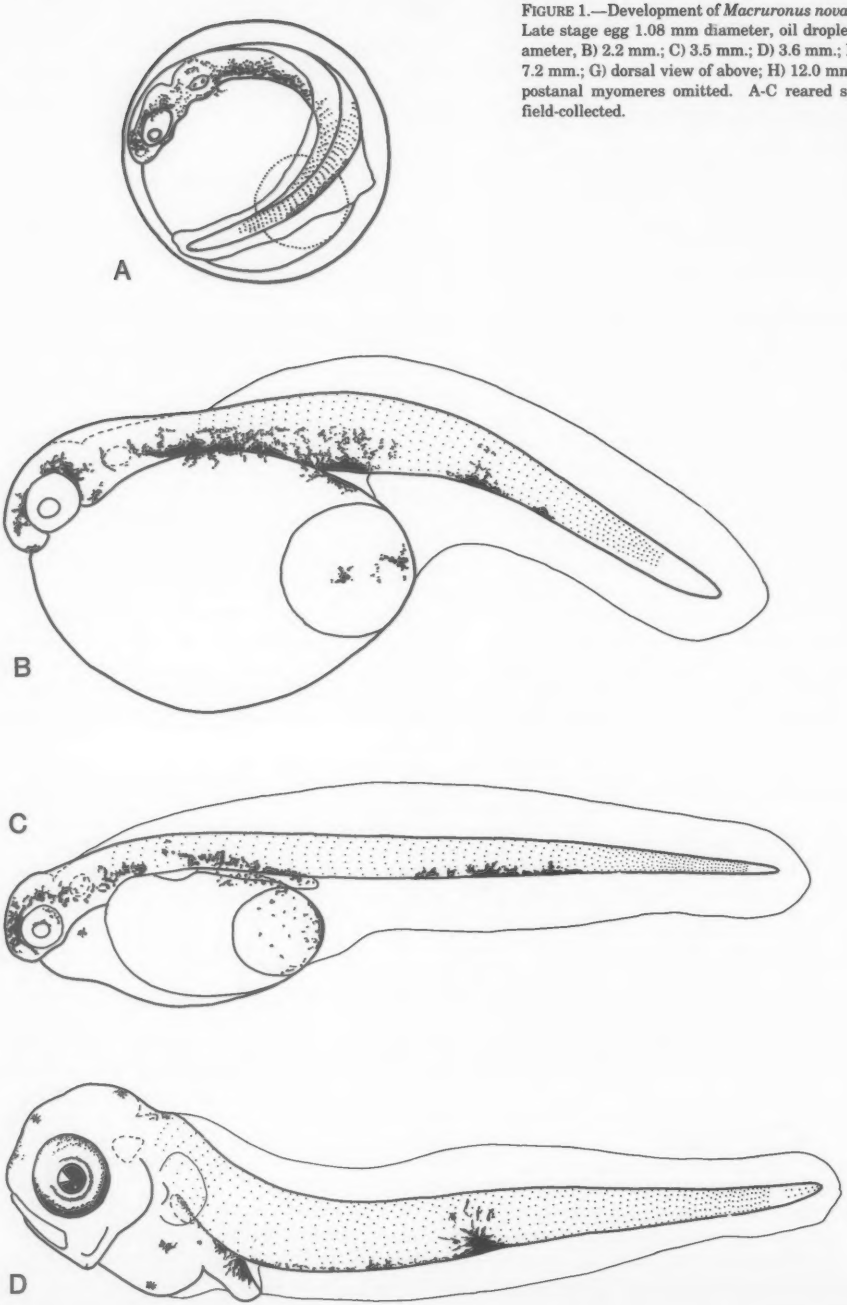
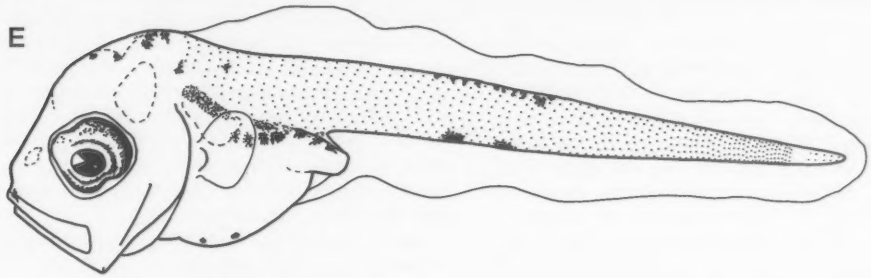


FIGURE 1.—Development of *Macruronus novaezelandiae:* A) Late stage egg 1.08 mm diameter, oil droplet 0.37 mm diameter, B) 2.2 mm.; C) 3.5 mm.; D) 3.6 mm.; E) 5.3 mm.; F) 7.2 mm.; G) dorsal view of above; H) 12.0 mm.; I) 24.2 mm. postanal myomeres omitted. A-C reared specimens, D-I field-collected.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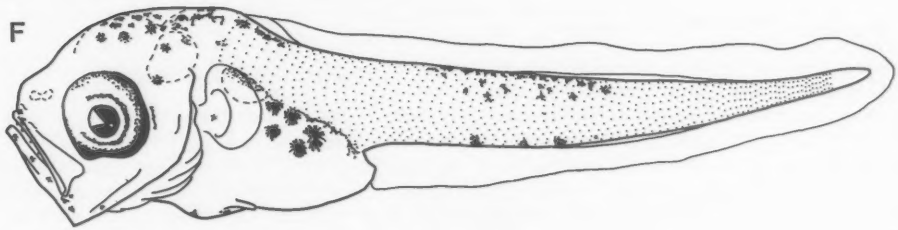
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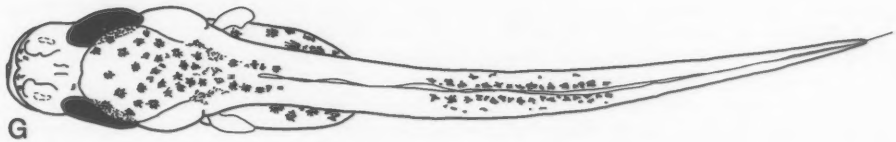
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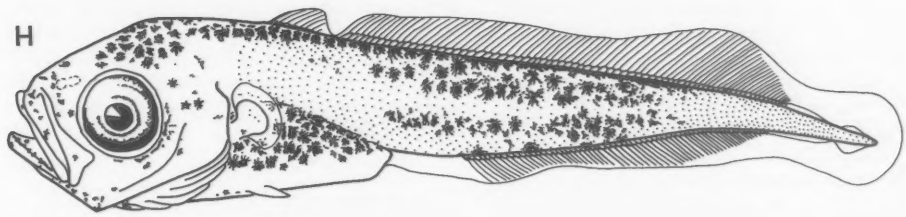
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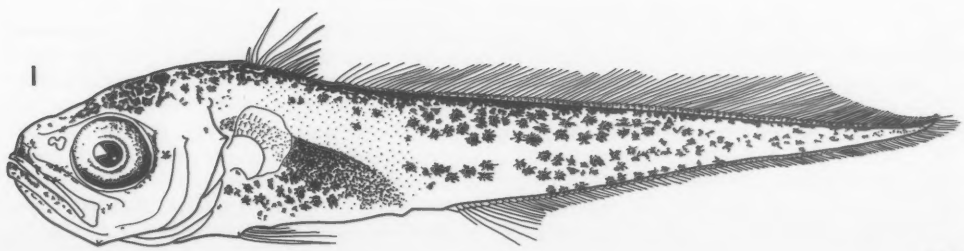
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The onset of dentary pigment is variable; no pigment may be present on some larvae as large as 7.0 mm. Most larvae develop 1 or 2 melanophores over the posterior section of the dentary by 5.3 mm and add melanophores anteriorly along its length, with 5 or 6 usually present by 7.1 mm.

Two melanophores are often present around the otic capsule by 7.0 mm, but they are obscured by overlying tissue in 10.0 mm larvae. Scattered melanophores develop over the pterotic region by 25.0 mm, but the operculum and preoperculum remain largely unpigmented, even in the largest specimen examined (34.2 mm).

Trunk and Tail Pigmentation

Newly hatched larvae have melanophores on the body above the yolk sac and ventrally on the tail. Some pigment is also present on the yolk sac near the developing gut and scattered over the oil droplet. Pigment forms a cap over the gas bladder by 4.2 mm. Melanophores are gradually added to the lateral surfaces of the gut throughout the larval period until the entire gut (including the ventral surface) becomes pigmented by 30.0 mm.

Dorsal pigment first appears on larvae 3.8–4.5 mm as scattered melanophores at approximately 60% NL. Melanophores rapidly increase in number and form a double row, extending from 51% to 67% NL in larvae of 5.0 mm. Lateral melanophores may also develop above the body midline in this region. Concurrently, a similar double row of melanophores appears and extends posteriorly from the head (Fig. 1G). The head and tail rows join by 10.5 mm. Melanophores appear posteriorly in the caudal region by 29.0 mm forming a twin series one either side of the developing dorsal fin. Pigment also appears internally on the dorsal surface of the vertebrae in larvae of 9.5 mm and extends anteriorly to approximately 50% SL and posteriorly to the last vertebrae by 34.0 mm.

Single melanophores appear on the dorsal fin ray bases by 14.0 mm and are present on all bases by 29.0 mm.

Pigment along the ventral midline of the tail appears in newly hatched larvae as a diffuse region that extends posteriorly from the yolk sac to 75–82% NL. This contracts to 1–3 melanophores (most commonly 2) located 52–65% NL in larvae of 3.8–4.0 mm. Additional melanophores (up to 6) may appear later, but the initial 1–3 melanophores persist throughout the larval period. In larvae larger than 7.0 mm, the initial 1–3 melanophores appear internally above the anal fin ray bases and are gradually obscured by both overlying musculature and external melanophores. These ventral melanophores on the tail are a useful diagnostic character, although their appearance varies, depending on their degree of expansion. This variability in melanophore appearance is particularly evident in small larvae where expanded ventral melanophores may extend over the lateral surfaces of the body to almost the dorsal area (Figs. 1D, 2).

Lateral pigment gradually intensifies throughout the larval period, excepting the area immediately above the gut, which remains largely devoid of pigment even in the largest specimen (34.2 mm).

Morphological Variability

Macruronus novaezelandiae larvae showed some size variation in development. In general, specimens captured in ring net and RMT samples appeared to develop features at slightly smaller sizes than those taken from drop net samples. This is likely a result of differential shrinkage of specimens caught by the different capture systems. Hay (1981) reported that considerably more shrinkage occurred in Pacific herring when larvae were killed prior to fixation and that shrinkage increased with tow length. Ring net and RMT tows varied in duration from 15 to 110 minutes, with most larvae dead by the time the net was retrieved and the catch fixed. Drop net sampling, in contrast, lasted for, at most, 3 minutes duration, and many larvae were still alive on fixation. Some variability in development can also be expected in field-collected larvae as a reflection of past history (e.g., feeding success), although it is unlikely such variations would account for the observed differences between larvae caught by different techniques.

Meristics and Osteology (Table 2)

Head and Axial Skeleton

In laboratory-reared larvae, jaw development was first visible after 3.5 days (posthatch) with a functional mouth present in larvae of 5.5 days (3.7 mm). Pigmentation of the eyes also occurred at this time suggesting that larvae were ready for first feeding. The smallest larva stained was a field-collected specimen 3.7 mm NL. The maxilla, premaxilla, dentary, and cleithrum were all ossified in this specimen.

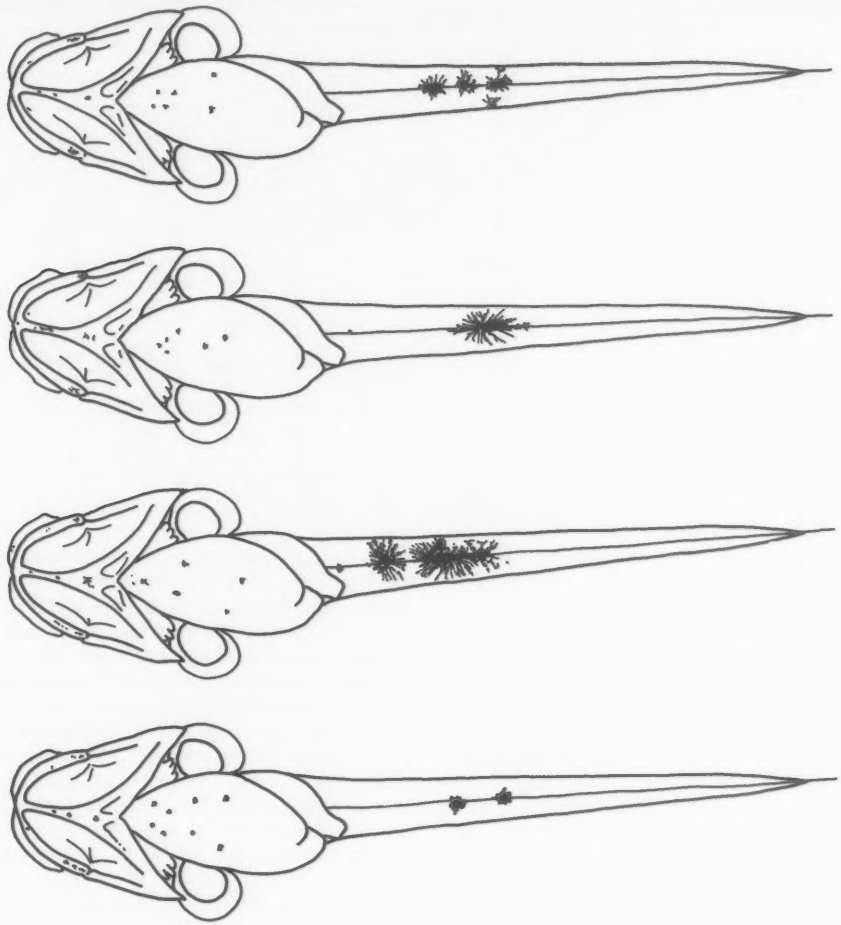

FIGURE 2.—Variability of ventral pigment on the tail in 4.9 mm larvae of *Macruronus novaezelandiae*.

Ossification of branchiostegals begins in larvae of 4.6 mm, with the full complement of 7 ossified by 11.5 mm. Gill rakers are first discernible in larvae of 9.4–9.9 mm with the full complement of 7 + 22 – 23 present by 28.9 mm.

Ossification of neural and haemal spines generally precedes that of the vertebral centra. Ossification of centra, neural spines, and haemal spines occurs sequentially from anterior to posterior proceeding slowly in larvae less than 9.0 mm in length and then more rapidly until the full complement is ossified by 23.2 mm. Elements associated with the caudal complex are the last to ossify.

Fins

Completion of fin development in *M. novaezelandiae* occurs in the sequence: first dorsal and pelvic (almost simultaneously), anal, second dorsal, caudal, pectoral.

Pelvic fins first appear in larvae of 5.7–5.8 mm as slight swellings either side of the gut. They do not form distinct buds until 6.9 mm. Ossification

TABLE 2.—Meristic counts from cleared and stained larval and juvenile *Macruronus novaezelandiae*. Specimens between dashed lines are undergoing notochord flexion. a = specimen damaged; b = juveniles not stained.

Length (mm)	Fin rays				Branchiostegal rays	Gill rakers			Total centra	Neural spines	Haemal spines	Caudal elements
	dorsal	anal	pectoral	pelvic		upper	lower	total				
3.7	—	—	—	—	—	—	—	—	—	—	—	—
3.9	—	—	—	—	—	—	—	—	—	1	—	—
4.2	—	—	—	—	—	—	—	—	—	1	—	—
4.6	—	—	—	—	1	—	—	—	—	2	—	—
4.8	—	—	—	—	1	—	—	—	—	2	—	—
5.2	—	—	—	—	3	—	—	—	—	2	—	—
6.0	—	—	—	—	3	—	—	—	—	3	—	—
7.4	—	—	—	—	5	—	—	—	5	6	—	—
9.4	4 + 28	18	—	3	6	—	8	8	42	55	37	—
9.9	0 + 19	4	—	—	6	—	6	6	38	54	34	—
11.5	9 + 74	60	—	4	7	—	12	12	55	58	42	—
16.3	12 + 84	73	4	8	7	1	15	16	70	70	55	3
17.4	12 + 86	76	4	8	7	3	15	18	71	70	55	3
19.8	13 + 87	86	3	8	7	5	15	20	73	74	57	4
23.2	12 + 100	90	9	8	7	5	17	22	76	74	57	5
26.1	13 + 99	90	13	8	7	5	21	26	76	74	57	5
28.9	13 + 99	91	9	8	7	7	22	29	78	76	57	a
188	13 + 94	90	20	8	7	7	22	29	b	b	b	b
190	13 + 96	90	20	8	7	7	23	30	b	b	b	b

may start as early as 9.4 mm with the full complement (8 rays) present by 16.3 mm. Ossification proceeds from the outer to the innermost rays.

The second dorsal fin anlage is visible in larvae of 5.7 mm. Bases are first visible by 6.9 mm, with ray ossification commencing by 7.3 mm. Although the anal fin anlage does not form until 6.9 mm, complete ossification is reached before that of the second dorsal. Distinct anal fin bases are first visible in 7.2 mm larvae and ossification has consistently begun by 9.9 mm. The full complement of anal rays is present by 21.0 mm and for the second dorsal, by 23.2 mm.

The first dorsal starts development slightly later than the second dorsal, although it is the first fin to complete ossification. The full complement of 12 or 13 elements is present by 16.3 mm.

Pectoral buds were first observed in larvae 4.5 days posthatch (3.2 mm). However, the pectoral fin is the last to complete development. Ossification of pectoral rays starts by 16.3 mm; a 34.2 mm specimen had only 15 ossified rays, still short of the 20 rays of juveniles. Sequence of ossification is from upper to lower.

The caudal fin anlage first appears on the ventral surface of the notochord just anterior to the tip in larvae of 10.4 mm. Flexion begins at 20 mm and is usually complete by 28 mm. Ossification of all caudal elements was incomplete in a 34.2 mm specimen. Insufficient material of the appropriate size was available to define the completion of caudal ossification.

The caudal complex in *M. novaezelandiae* is based on two ural centra, two epurals, a superior hypural (HP3 + 4), inferior hypural (HP1 + 2), and a parhypural (Fig. 3). Eight to nine rays articulate with these elements—one or two rays on the second epural, three rays on the superior hypural, two on the inferior hypural, and one ray each on the first epural and the parhypural. Single rays also articulate with the elongate neural and haemal spines of the first preural centrum. X and Y bones are present although they are not readily distinguishable from dorsal and anal pterygiophores. Total caudal fin ray counts are low (12 or 13).

Additional caudal structures occurred in one of the six specimens examined. This specimen had a twin haemal spine on the first preural centrum and greatly elongated haemal spines on preural centra 3–8 (1.3–1.4 times the length of corresponding neural spines, Fig. 3).

DISCUSSION

The general morphology and pigmentation of *M. novaezelandiae* larvae show broad similarities to *Merluccius* and to gadine gadids. Characteristic differences between *M. novaezelandiae* and *Merluccius* species occur in fin structure and the sequence of fin development. In *Merluccius*, the caudal fin is the first to form, followed by the pelvic. In *Macruronus*, caudal development is late with the caudal fin being the second last to

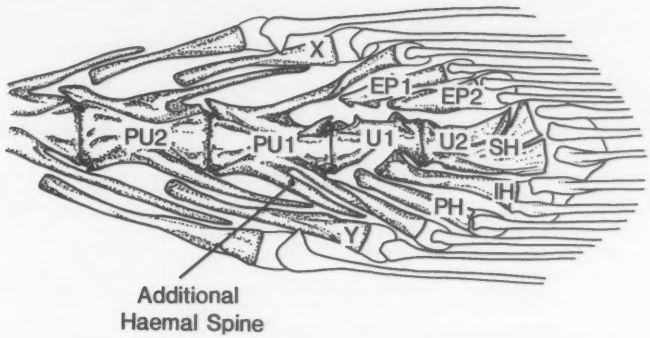

FIGURE 3.—Caudal osteology of a juvenile *Macruronus novaezelandiae* (181 mm SL). X = X bone, Y = Y bone, EP = epural, SH = superior hypural (hypurals 3+4), IH = inferior hypural (hypurals 1+2), PH = parhypural, U = ural centra, PU = preural centra.

form. The pectoral fin in *Macruronus* larvae is more markedly stalked than in *Merluccius*. Fahay and Markle (1984) suggested that this pectoral modification in larvae with delayed caudal development may be a compensatory response associated with swimming.

Although the larvae of the remaining merlucciid genera (*Lyconus* and *Lyconodes*) are currently unknown, fin structure and position should be useful in separating these from *Macruronus*. Based on adult features, pelvic insertion should distinguish *Macruronus* (pelvics inserted behind pectorals) from *Lyconus* (opposite) and *Lyconodes* (abdominal). Additionally, *Lyconus* has only a single dorsal fin and no caudal fin.

The caudal fin of *M. novaezelandiae* is similar to *Muraenolepis* in its confluence with dorsal and anal fins (Fahay and Markle 1984). This similarity extends to the undifferentiated X and Y bones and the total caudal fin ray count (12 or 13) reported by these authors. However, unlike *Muraenolepis*, *M. novaezelandiae* has radials fused to the spines of the first preural centrum, which is the more typical gadoid condition.

Variability in the structure and appearance of bones associated with the caudal fin has been reported for other *Macruronus* species. Marshall (1966) observed double neural arches and "supernumary elements" in *M. magellanicus*. Indeed, variability in gadiform caudal structure appears not to be unusual with examples in several taxa (Markle 1982). Unfortunately, insufficient specimens in the appropriate 35–150 mm size range were available to assess developmental characteristics of these variations in blue grenadier.

ACKNOWLEDGMENTS

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NOTE: Since the acceptance of this paper, the embryological work by A. Patchell (see section on Development) has been published in New Zealand Journal of Marine and Freshwater Research Vol. 21, No. 2. That paper includes a similar larval developmental sequence to that reported here.

LITERATURE CITED

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THE DISTRIBUTION, ABUNDANCE, AND TRANSPORT OF LARVAL SCIAENIDS COLLECTED DURING WINTER AND EARLY SPRING FROM THE CONTINENTAL SHELF WATERS OFF WEST LOUISIANA[1]

JAMES H. COWAN, JR.[2] AND RICHARD F. SHAW[3]

ABSTRACT

The larvae of six species of Sciaenidae were collected in continental shelf waters off west Louisiana on five midmonthly ichthyoplankton cruises from December 1981 to April 1982. Ranked in order of abundance these species were sand seatrout, *Cynoscion arenarius*; Atlantic croaker, *Micropogonias undulatus*; spot, *Leiostomus xanthurus*; black drum, *Pogonias cromis*; southern kingfish, *Menticirrhus americanus*; and banded drum, *Larimus fasciatus*. Total larva density was highest in April, and the high densities were associated with the coastal boundary layer, a horizontal density front caused by an intrusion of fresher water onto the inner shelf that probably issued from the Atchafalaya River east of the study area. Spawning by sand seatrout began in January, two months earlier than previously reported, and first occurred offshore of midshelf but moved shoreward as the season progressed. Analysis of length-frequency data suggest that spot probably began to spawn in November, one month earlier than once thought. Both sand seatrout and Atlantic croaker larvae were captured at higher rates at night than during the daytime. Sand seatrout larvae appear to be somewhat surface oriented while spot may undergo vertical migration. Interpretation of the sciaenid data support a previously developed transport hypothesis involving gulf menhaden larvae and west-northwest alongshore advection within and just outside of a horizontally stratified coastal boundary layer.

Members of the perciform family Sciaenidae are an important sport and commercial fishery resource along the United States coast of the Gulf of Mexico and are perhaps the most prominent group of northern Gulf inshore fishes. Sciaenids exceed all other families in numbers of species (18) and in numbers of individuals or biomass; they are among the top four families with Mugilidae, Engraulidae, and Clupeidae (Gunter 1938, 1945; Moore et al. 1970; Franks et al. 1972; Hoese and Moore 1977). Of the six species of sciaenids captured during this study, only the banded drum, *Larimus fasciatus*, is not commonly sought by both sport and commercial fishermen.

Many of Louisiana's sciaenids spawn in coastal or offshore waters. They have pelagic eggs and young which are then transported into estuaries (Johnson 1978 for review). The seasonal importance of Louisiana's estuaries as nursery grounds for postlarval and juvenile sciaenids is well documented (Cowan 1985 for review), and several summary works are available which contain taxonomic and biological information on adult sciaenids (Pearson 1929; Suttkus 1955; Guest and Gunter 1958; Hoese and Moore 1977; Johnson 1978; Powles and Stender 1978; Barger and Johnson 1980; Barger and Williams 1980; Mercer 1984a, b). In contrast, there is little information about sciaenid ichthyoplankton assemblages in Gulf continental shelf waters, their offshore and coastal distribution, or the oceanic current systems which influence their estuarine recruitment.

This study provides such early life history information by determining larva distribution, abundance, and length frequency; by documenting spawning location (depth and distance from shore) of winter and early spring-spawned sciaenids off west Louisiana; and by analyzing larval sciaenid distribution with respect to known water circulation patterns and a larval gulf menhaden, *Brevoortia patronus*, transport hypothesis in the shelf waters of the northwestern Gulf of Mexico (Shaw et al. 1985b). Recruitment implications of the observed distribution, larva age structure, and transport of sciaenids in Louisiana waters are also discussed.

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[2]Center for Wetland Resources, Louisiana State University, Baton Rouge, LA 70803-7503; present address: Center for Environmental and Estuarine Studies, University of Maryland, Chesapeake Biological Laboratory, Box 38, Solomons, MD 20688-0038.

[3]Center for Wetland Resources, Louisiana State University, Baton Rouge, LA 70803-7503.

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METHODS AND MATERIALS

Detailed sampling methodology has been presented elsewhere (Shaw et al. 1985 a, b). Briefly, larval sciaenids were collected off west Louisiana on a sampling grid consisting of 37 stations on 5 transects (Fig. 1) during 5 midmonthly cruises from December 1981 to April 1982. Ichthyoplankton samples were analyzed from the 335 μm mesh net side of an opening and closing, 60 cm, paired "bongo type" plankton sampler fitted with General Oceanics[4] flowmeters (model no. 2030). Most plankton collections (125 of 187 total) consisted of 10-min stepped oblique tows from near bottom to surface. Nets were set closed and opened just prior to the stepped ascent. Each tow had five steps with a retrieval rate between steps of 20 m/minute; towing speed was about 1 m/second (2 knots). The object of the 10-min tow was to filter approximately 100 m^3 of water. This process increased the water volume filtered per unit depth at the shallow stations relative to deeper stations. This discrepancy is acceptable since the alternative would be to compare 17-s shallow-station oblique tows with 9-min deep-station tows at a uniform retrieval rate (Houde 1977). At selected stations (A-3, 6, 9; B-1; C-6; D-1; E-3, 6, 9; Fig. 1), only 10-min simultaneous surface and near-bottom horizontal tows (31 surface and 31 near-bottom) were made to determine if sciaenid larvae were vertically stratified. Larva total length (TL) was measured to the nearest 0.1 mm. Larva densities are reported as standardized catch rates at a station (density = larvae/100 m^3).

A four-way analysis of variance (ANOVA) was performed on $\log_{10}$ transformed [(no. larvae/100 m^3) + 1] data to determine the spatial (vertical and horizontal), temporal, and diel patterns of species density and distribution. The four main effects tested were month (January–April); station depth group (d.g.) (d.g. 1 ≤ 10 m, 10 m < d.g. 2 ≤ 14 m, 14 m < d.g. 3 < 24 m and d.g. 4 ≥ 24 m); day-night (2000 hours ≤ night ≤ 0500 hours); and horizontal tow type (surface vs. near-bottom). Data from the December cruise were not included as only the A transect was completed due to adverse weather conditions.

Two methods of current estimates were utilized (following Shaw et al. 1985b): 1) instantaneous current profiles taken at each station and 2) continuous surface and near-bottom current meter measurements at two sites (H and S; Fig. 1). The instantaneous number of larvae transported on each transect was calculated by using the equation $D \times \overline{U} \times M$ = number of larvae per meter per second where D = larva density (larvae/m^3) from either oblique tows or from the mean of the horizontal tows (i.e., average of surface and near-bottom catch rates), $\overline{U}$ = depth-averaged water velocity (m/s) determined from instantaneous current meter profiles at each station, and M = water depth (m) at each station.

Distribution diagrams and length-frequency histograms were generated for each cruise for the three most abundant sciaenid species. Inspection of these data along with current measurements allowed a comparison with the previously mentioned transport hypothesis.

RESULTS AND DISCUSSION

Total Sciaenids

A total of 5,225 larval sciaenids accounted for 9.1% of the fish larvae collected. In December through February, samples were dominated by Atlantic croaker, *Micropogonias undulatus*, and spot, *Leiostomus xanthurus*. In March and April samples contained mostly sand seatrout, *Cynoscion arenarius*. In all, six species of sciaenid larvae were collected: sand seatrout (N = 4,100); Atlantic croaker (N = 567); spot (N = 264); black drum, *Pogonias cromis* (N = 68); southern kingfish, *Menticirrhus americanus* (N = 53); and banded drum (N = 13). Additional *Menticirrhus*, not identifiable to species, accounted for 160 more specimens (Table 1). A more detailed examination of the data on the three most abundant sciaenid species follows.

Sand seatrout, *Cynoscion arenarius*

A total of 4,100 sand seatrout larvae was collected making it the most abundant sciaenid taken during the study. Larval sand seatrout densities were highest in April (Table 1) with a mean of 46.1 larvae/100 m^3; mean density in February and March was 0.3 and 2.9/100 m^3, respectively, and 1 larva was collected in January. Larvae were distributed mostly over the midshelf in February but highest concentrations were later found inshore and towards the east (Fig. 1). Over the course of study, larvae were found in temperatures and salinities ranging from 14° to 21°C and

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Services, NOAA.

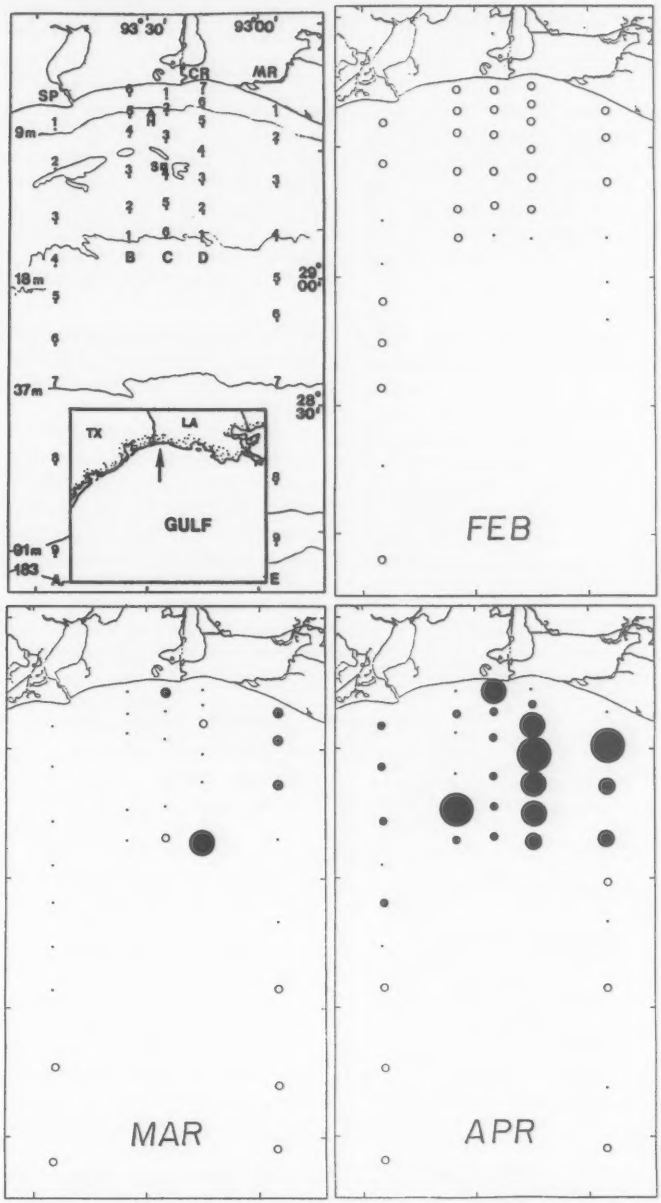


FIGURE 1.—Density distribution of sand seatrout, *Cynoscion arenarius*, larvae by month, February–April 1982. Densities are as follows: o = 0; · >0–10; • >10–50; ● >50–99; ● >99–250; ● >250/100 m^3 of water filtered from all plankton tow types. Also shown is the station sampling grid with moored current meter sites (H and S) and selected isobaths. SP = Sabine Pass, CR = Calcasieu River, and MR = Mermentau River.

TABLE 1.—Total number, months of occurrence and monthly density of sciaenid larvae collected in west Louisiana shelf waters from December 1981 to April 1982.

Taxa	Total number	Months of occurrence and density (No./100 m³)				
		Dec.	Jan.	Feb.	Mar.	Apr.
Cynoscion arenarius	4,100	—	1 larva	0.3	2.9	46.1
Micropogonias undulatus	567	2.0	2.2	3.2	2.2	0.2
Leiostomus xanthurus	264	7.8	1.3	0.9	0.1	—
Menticirrhus sp.	160	—	—	—	—	1.9
Pogonias cromis	68	—	1 larva	0.5	0.2	0.2
Menticirrhus americanus	53	—	—	—	—	0.6
Larimus fasciatus	13	—	—	—	—	0.2

from 15 to 36 ppt (Table 2) and at station depths ranging from 5 to 70 m, but most were collected inside the 18 m isobath. Larval sand seatrout density increased in April with many stations exhibiting densities in excess of 250 larvae/100 m³; the larvae appeared to be associated with a freshet of water on the shelf, probably issuing from the Atchafalaya River east of the study area (Shaw et al. 1985a). The presence of riverine runoff on the shelf, which was most evident in March and April 1982, caused the development of an oceanic salinity front referred to as the coastal boundary layer, 10–35 km from shore (Wiseman et al. 1987).

Observed spawning seasonality and location for sand seatrout are in part consistent with previously published information (Shlossman and Chittenden 1981 for review). The presence of a 4 mm TL larva in January indicates some spawning had taken place at least 2 months earlier than

TABLE 2.—Monthly data summaries at time of capture for three sciaenid larvae (*Cynoscion arenarius*, *Micropogonias undulatus*, and *Leiostomus xanthurus*) collected in west Louisiana shelf waters from December 1981 to April 1982.

Species/month	Total number	Length range (mm TL)	Temperature range (°C)	Salinity range (ppt)	Depth range (m)
Cynoscion arenarius					
January	1	4	14	35	18
February	20	2.5–4.5 (mode = 2–3)	14–20	34–36	15–70
March	203	1.5–10.5 (mode = 2–3)	14–18	25–36	5–40
April	3,876	1.5–20.5 (mode = 2–3)	20–21	15–36	5–70
Micropogonias undulatus					
December	28	2.5–10.5 (mode = 3–4)	12–20	30–36	10–65
January	158	2.5–10.5 (mode = 4–5)	10–18	30–36	5–70
February	221	2.5–17.5 (mode = 14–15)	11–17	27–36	5–40
March	144	2.5–19.5 (mode = 14–15)	14–20	25–36	5–115
April	16	11.5–18.5 (mode = 17–18)	20.5	22	7
Leiostomus xanthurus					
December	110	2.5–7.5 (mode = 3–4)	14–18	30–36	16–65
January	89	2.5–13.5 (mode = 4–5)	10–18	30–36	5–40
February	62	3.5–15.5 (mode = 12–13)	10–17	28–36	5–40
March	3	3.5–16.5	14–17.5	26–36	11–40

previously reported. Monthly length-frequency data for sand seatrout show that larvae as large as 11 mm TL were first present in March samples (Fig. 2A). Based on the estimated growth rate determined for sand seatrout (Cowan 1985; Shaw et al., in press), an 11 mm larva could be as old as 65 days; this further supports January spawning. Sand seatrout are reported to spawn from March to August, during two discrete periods—one in March–May, the other August–September, with little spawning between the two peak periods (Hoese 1965; Daniels 1977; Shlossman and Chittenden 1981).

An examination of distribution and length-frequency data (Figs. 1, 2A) suggests that most spawning initially took place in midshelf to offshore waters at depths ranging from 15 to 80 m or to about 175 km from shore. As the season progressed into March and April, spawning location, as determined by the presence of larvae <3.0 mm TL, was more inshore (5–18 m) with few small larvae occurring at depths >25 m.

Other than the indication that spawning may move from offshore to inshore waters as the season progresses, this spatial information agrees with the limited life history data available on sand seatrout. Most spawning has been shown to occur in the shallow waters of the Gulf of Mexico, primarily between 7 and 15 m in depth (Gunter 1945; Moffet et al. 1979; Shlossman and Chittenden 1981). Running ripe *C. arenarius* have been captured in deepter waters (70–90 m) in February and March, but no spawning was indicated (Franks et al. 1972; Perry 1979).

In a four-way ANOVA employed to determine patterns of larval sand seatrout density and distribution, month was a highly significant main effect ($P < 0.01$; Table 3) reflecting spawning seasonality and the magnitude of the density increase in April. The test for interaction between month and day-night was employed to determine if daytime gear avoidance was evident as size and mobility of larva increased. Most sand seatrout collected, however, were small and no clear monthly modal increase in larva size was evident (Fig. 2A). The significant interaction ($P < 0.01$) was probably due to an increased catch in oblique tows at night as the season progressed (0.0 in January, 64.9/100 m^3 in April). The significant interaction between month and depth group and the highly significant depth group main effect ($P < 0.01$) represents the shift in larva concentration from midshelf early in the study, to a more coastal distribution in March and April (Fig. 1). Mean larva density was greatest in depth group 1 (23.7/100 m^3) followed by depth groups 2, 3, and 4 (12.7, 9.2, and 0.3/100 m^3, respectively). The third main effect, day vs. night tows, was highly significant ($P < 0.01$); many more sand seatrout larvae were collected at night (averge catch rates in all night (74) tows combined = 21.6/100 m^3 vs. day (113) tows = 7.4/100 m^3). Highest nighttime catches occurred in oblique (49) tows (26.9/100 m^3) while the day-oblique-catch rate averaged 7.6/100 m^3 in 76 tows. Overall, average catch rate was highest in oblique (125) tows (14.6 larvae/100 m^3), followed by surface (31) tows (9.2/100 m^3), and then bottom (1.9/100 m^3; 31 tows). Intrepretation of the data suggests that

TABLE 3.—Summary data from four-way analysis of variance done on $\log_{10}$ transformed [(larvae/100 m^3) + 1] data from ichthyoplankton samples collected from January to April 1982. The results are for A. *Cynoscion arenarius*, B. *Micropogonias undulatus*, and C. *Leiostomus xanthurus*. The four main effects tested were months (Jan.–Apr.), station depth group (d.g. 1 ≤ 10 m, 10 m < d.g. 2 ≤ 14 m, 14 m < d.g. 3 < 24 m and d.g. ≥ 24 m), day - night (2000 hours ≤ night ≤ 0500 hours) and horizontal tow type (surface vs. near-bottom).

Source	df	PR > F	
A. Dependent variable:			
$\log_{10}$ [(*Cynoscion arenarius*/100 m^3) + 1]			
Model	21	0.0001**	$r^2 = 0.75$
Month	3	0.0001**	
Depth group	3	0.0001**	
Day-night	1	0.0026**	
Horizontal tow type	1	0.2574 (NS)	
Month vs. Day-night	3	0.0001**	
Month vs. Depth group	9	0.0001**	
Day-night vs. Tow type	1	0.4180 (NS)	
Error	177		
Corrected Total	198		
B. Dependent variable:			
$\log_{10}$ [(*Micropogonias undulatus*/100 m^3) + 1]			
Model	21	0.0001**	$r^2 = 0.63$
Month	3	0.0045**	
Depth group	3	0.3551 (NS)	
Day-night	1	0.0001**	
Horizontal tow type	1	0.4448 (NS)	
Month vs. Day-night	3	0.2168 (NS)	
Month vs. Depth group	9	0.0001**	
Day-night vs. Tow type	1	0.1288 (NS)	
Error	177		
Corrected Total	198		
C. Dependent variable:			
$\log_{10}$ [(*Leiostomus xanthurus*/100 m^3) + 1]			
Model	21	0.0001**	$r^2 = 0.51$
Month	3	0.0001**	
Depth group	3	0.0033**	
Day-night	1	0.1875 (NS)	
Horizontal tow type	1	0.3216 (NS)	
Month vs. Day-night	3	0.2138 (NS)	
Month vs. Depth group	9	0.0001**	
Day-night vs. Tow type	1	0.0324*	
Error	177		
Corrected Total	198		

* = Statistically significant ($P < 0.05$).
** = Highly significant ($P < 0.01$).
(NS) = Not significant.

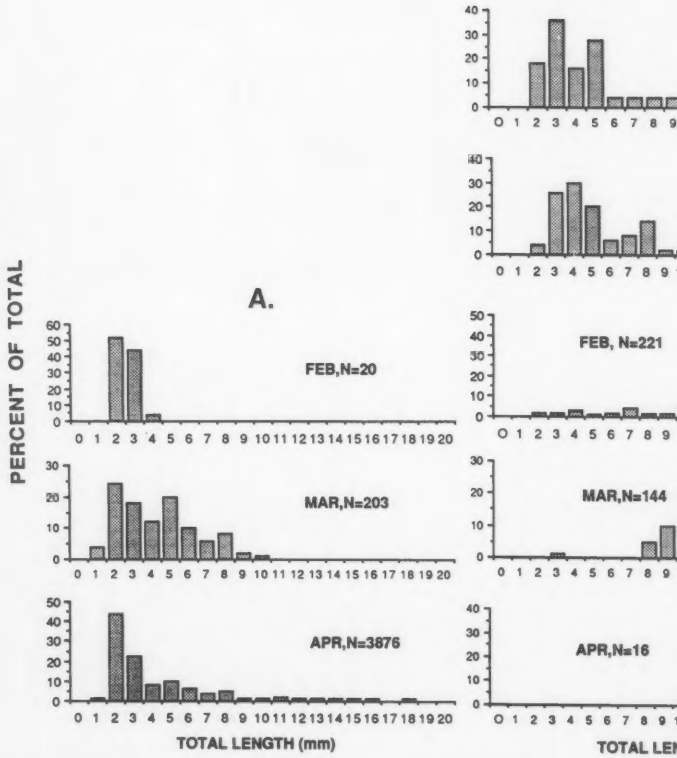
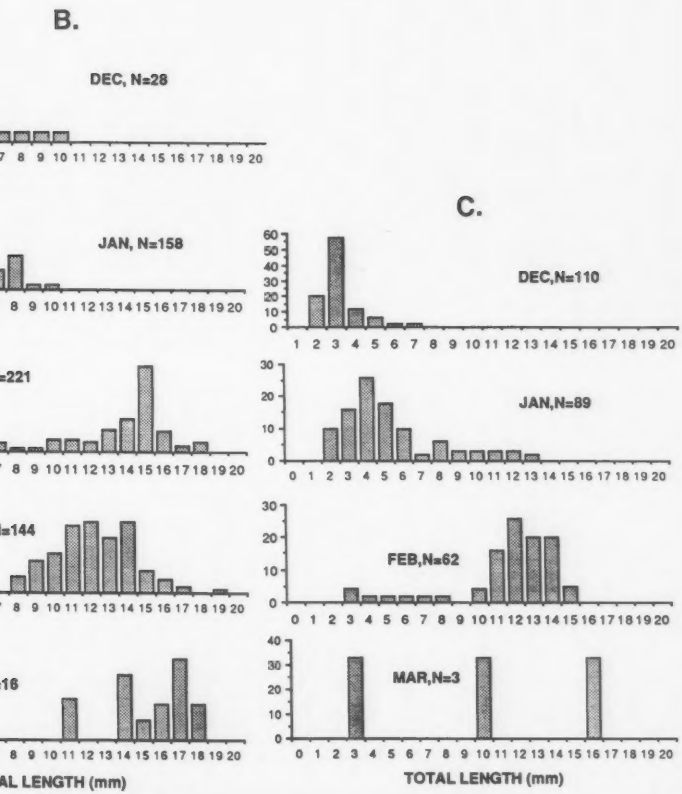


FIGURE 2.—Length-frequency data by month for larval sciaenids, December–April 1982. A. *Cy*
number caught and



A. *Cynoscion arenarius*, B. *Micropogonias undulatus*, and C. *Leiostomus xanthurus*. N = total
ght and measured.

sand seatrout larvae were somewhat surface oriented.

Atlantic croaker, *Micropogonias undulatus*

The second most abundant sciaenid taken was Atlantic croaker ($N = 567$). Larval Atlantic croaker density was greatest in February at 3.2/100 m^3, but density was relatively constant from December through March (Table 1). Mean densities for December, January, March, and April were 2.0, 2.2, 2.2, and 0.2/100 m^3, respectively. Atlantic croaker was the only sciaenid collected in all months of the study. Their overall distribution (all sizes combined) was generally uniform over most of the shelf (Fig. 3) except in March and April when they were more often found inshore. Recently spawned larvae (<3.0 mm TL) were also collected over much of the shelf at station depths ranging from 15 to 115 m or from about 20 to 200 km from shore. However, most small larvae were collected near midshelf about 65–125 km from shore. In December and January the majority of the larvae were small. By April, no recently spawned individuals were collected (Fig. 2B). For the study overall, larvae were found in salinities and temperatures ranging from 22 to 36 ppt and from 10° to 20.5°C (Table 2).

Spawning by Atlantic croaker in Gulf of Mexico waters is reported to occur from September to March, with a distinct peak in October (Hoese 1965; Sabins and Truesdale 1974; White and Chittenden 1977; Benson 1982) and to occur primarily offshore over a wide area (Pearson 1929; Hildebrand and Cable 1930; Wallace 1940; Haven 1957; Bearden 1964; Hoese 1965; Nelson 1967). Atlantic croaker larvae, however, have been taken on the outer continental shelf off Texas from September to May (Finucane et al. 1979).

As with sand seatrout, a four-way ANOVA was used to determine patterns in larva density and distribution (Table 3). Larval Atlantic croaker density by month was a highly significant main effect ($P < 0.01$). Densities at the end of their spawning period were low, increased only slightly in February, and then dropped off by April (Table 1). The interaction between month and day-night was not significant. The highly significant interaction between month and depth group was not surprising. Larvae were in more offshore waters early in the study while later becoming more abundant inshore (Fig. 3). However, as a main effect, depth group was not significant. Larval Atlantic croaker mean densities for depth groups 1 through 4 were 3.9, 0.8, 0.4, and 0.7/100 m^3, respectively. Day-night, as a main effect, was highly significant ($P < 0.01$). Larval Atlantic croaker density was over 5 times higher at night (all tow types combined) than during the day (3.7 vs. 0.7/100 m^3). However, the interaction between day-night and horizontal tow type was not significant. The fourth main effect tested, horizontal tow type, was not significant. Average catch rates at the surface and near-bottom were similar (1.0 and 1.8/100 m^3, respectively).

Spot, *Leiostomus xanthurus*

The third most abundant sciaenid collected was spot ($N = 264$). Density of spot larvae was highest in December at 7.8 larvae/100 m^3 (Table 1). However, the high December value must be viewed with a consideration of the abbreviated cruise track for that month and the resultant reduction in spatial coverage. Mean densities for January to March were 1.3, 0.9, and 0.1/100 m^3, respectively. No spot larvae were collected in April. In general, larva density was low and their distribution was uniform over the shelf out to the 40 m isobath, about 130 km offshore (Fig. 4). Spot were collected in temperatures and salinities ranging from 10° to 18°C and from 26 to 36 ppt (Table 2), and at stations with depths ranging from 5 to 65 m.

Larvae >7 mm TL in our mid-December (Fig. 2C) collections and small larvae (<3.0 mm TL) in all but the last cruise indicate that spawning probably began by at least November and continued through March. Spawning occurred from near midshelf (about 65 km) out to 175 km from the coast. Data presented here partly concur with previously published information on spot spawning periodicity. In the northern Gulf, spawning reportedly occurs from late December to March, peaking in January, and takes place well offshore in moderately deep water (Pearson 1929; Kilby 1955; Townsend 1956; Dawson 1958; Springer and Woodburn 1960; Pacheco 1962; Nelson 1967; Joseph 1972; Music 1974; Sabins and Truesdale 1974).

A four-way ANOVA indicated that month, as a main effect for spot larvae, was highly significant ($P < 0.01$), which probably reflects the decreasing catch rates seen from January to March (Table 3). The interaction between month and depth group was also highly significant ($P < 0.01$) as was depth group as a main effect. Larval spot

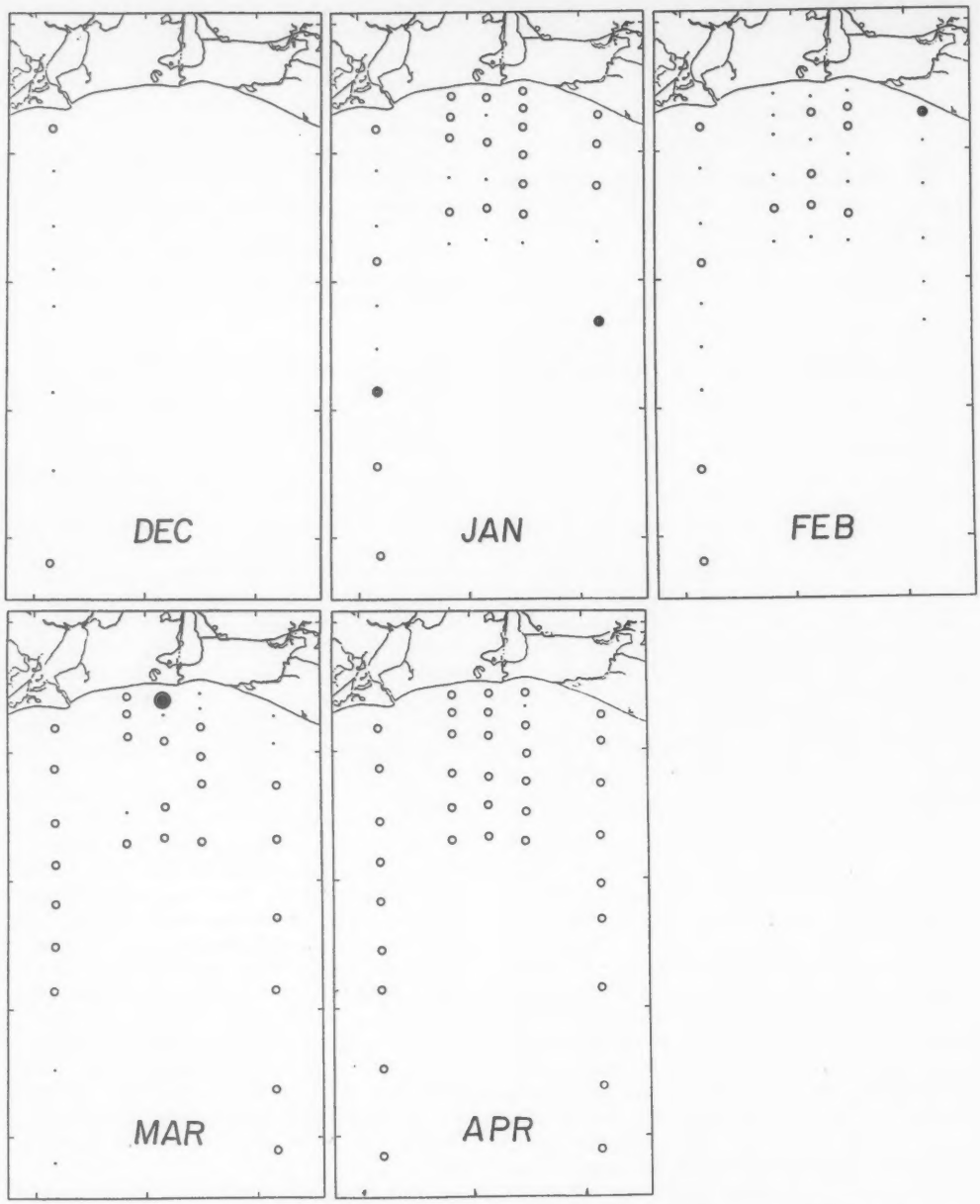


FIGURE 3.—Density distribution of Atlantic croaker, *Micropogonias undulatus*, larvae by month, December 1981—April 1982. Densities are as follows: o = 0; · >0–10; • >10–50; ● >50;–99; ● >99–250; ● >250/100 m^3 of water filtered from all plankton tow types.

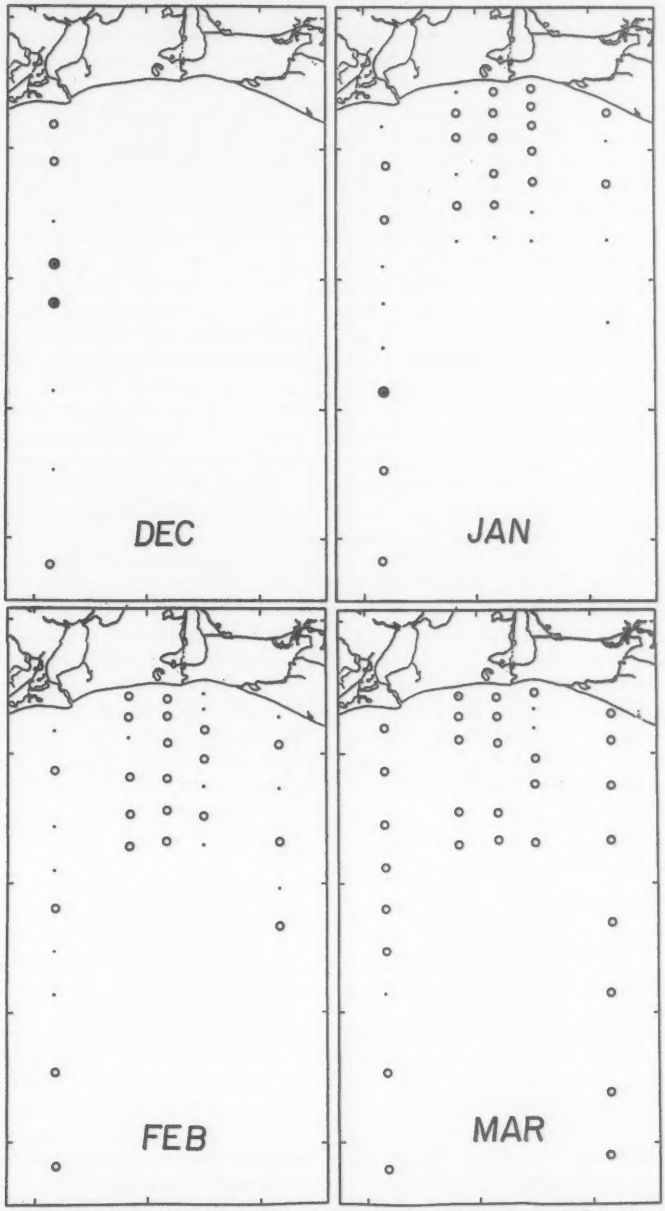


FIGURE 4.—Density distribution of spot, *Leiostomus xanthurus*, larvae by month, December 1981–March 1982. Densities are as follows: o = 0; · >0–10; • >10–50; ● >50–99; ● >99–250; ● >250/100 m^3 of water filtered from all plankton tow types.

densities were higher offshore in the early part of the study and then greater inshore during February and March. Depth group 4 had the highest mean density (1.3/100 m^3) followed by depth groups 1 and 3 (0.4/100 m^3 each) and depth group 2 (0.1/100 m^3). Day-night comparisons proved nonsignificant as a main effect for spot larvae. The average catch rates for all day and night tows were identical (0.5/100 m^3). However, the interaction between day-night and horizontal tow type was statistically significant ($P < 0.05$). In this case, vertical migration and stratification may be indicated. Average catch rate of spot larvae during the day at the surface was 0.1/100 m^3, while near the bottom it averaged 1.6. Conversely, nighttime average catch rate at the surface was 1.0/100 m^3, while the near-bottom rate averaged 0.04. These are very low densities but the vertical differences are an order of magnitude and their reversing pattern suggests that spot larvae were stratified and undergoing diel vertical migration. Daytime bottom and nighttime surface average catch rates were higher than for oblique (O) tows (day, O = 0.45/100 m^3; night, O = 0.49/100 m^3). Average catch rates for surface and near-bottom tows, regardless of time of day, were 0.5 and 0.9/100 m^3, respectively.

As previously mentioned, other larval sciaenid species (i.e., black drum, banded drum, southern kingfish) were collected during these cruises. However, relatively few individuals were captured (Table 1), making information on their distribution inconclusive.

TRANSPORT ANALYSIS

Alongshore advection within and just outside the coastal boundary layer in the northwestern Gulf of Mexico has been hypothesized as the major mechanism transporting gulf menhaden larvae to the estuaries in western Louisiana, rather than across-shelf transport from directly offshore. In contrast, such direct across-shelf transport has been demonstrated for sciaenids and other species along the U.S. mid-Atlantic coast (Nelson et al. 1976; Norcross and Austin 1981; Miller et al. 1984). The data collected for sciaenid larvae (all species combined) were examined in light of this Gulf hypothesis. Larval sciaenid densities were less than those for gulf menhaden but similarities in distribution were evident. Both larval sciaenid and gulf menhaden densities were highest at midshelf early in the study. By March and April the highest densities were found towards the east and inshore and were associated with a horizontal density front (coastal boundary layer) caused by an intrusion of fresher water onto the shelf.

The along-transect length-frequency patterns exhibited by larval sciaenids and gulf menhaden were also similar. No apparent increase in size was seen until gulf menhaden larvae were on the inner shelf or sciaenids were on the mid- to inner shelf. The expected pattern of a gradual increase in larva size from offshore to inshore, which would result if there were significant across-shelf (south to north) transport, was not evident in either data set. Off the North Carolina coast, Warlen (1981) and Miller et at. (1984) showed that ages and lengths of both spot and Atlantic croaker larvae increased systematically toward shore in an area where winter water currents favored across-shelf (west to east) transport.

During the winter of 1981–82, moored current meter data from sites H and S (Fig. 1) indicated that flow was directed primarily alongshore in the west-northwest direction. Several researchers have reviewed the circulation in the northwestern Gulf (Nowlin 1971; Kelly et al. 1982; Crout 1983). It was not until Cochrane and Kelly (1986) developed their comprehensive circulation model for the Louisiana-Texas continental shelf, however, that the ocean current patterns, which led to the hypothesized larva transport model, were fully documented. Flow in nearshore coastal waters is westward all year except in summer when it usually reverses, while farther offshore flow is eastward all year (Cochrane and Kelly 1986).

To quantify transport, larval sciaenid densities were combined with the vertically averaged, instantaneous current measurements. The resultant curves present the number of larvae transported per unit time at each station (Fig. 5). Early in the winter, highest sciaenid larva transport (mostly Atlantic croaker and spot) was located midshelf. Later (March and April), transport values were higher inshore and reflected the increase in larval sciaenid density (primarily sand seatrout). Overall, larva transport was primarily westward and ranged from about 0.05 to 4.0 larvae/meter per second.

Although the oceanographic data collected were insufficient to precisely quantify onshore transport rates, an estimate was obtained by using the mean current vectors from the near surface meter at site H (Fig. 1) from 24 January to 12 May 1982 (14.33 cm/second alongshore westward

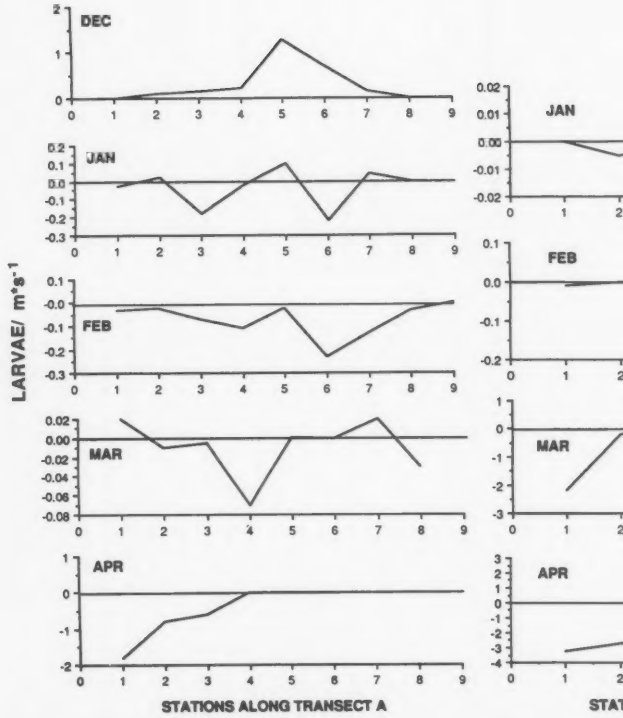
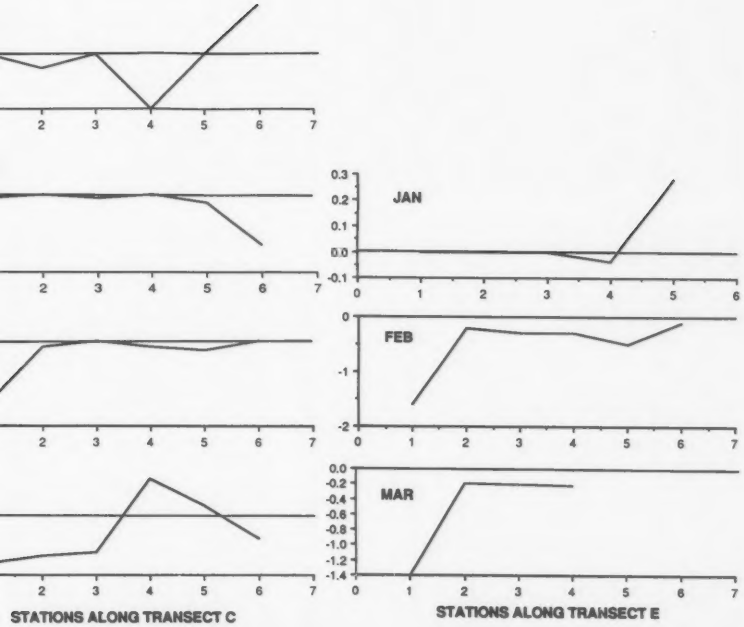


FIGURE 5.—Larval sciaenid transports (larvae/m·s) across transect A, C, and E, Decembe
1981–April 1982. Easterly transports are positive values. Transport rates were determine



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from the observed larva concentrations combined with instantaneous current measurements. Note the difference in scale between months.

and 1.75 cm/second shoreward). Based on that average shoreward advection rate we calculated that larvae could be passively transported 98 km in the onshore direction in 65 days. Examination of length frequency and age at capture data (Cowan, in press) suggest that larval Atlantic croaker arrive in nearshore coastal waters, on the average, 60–90 days after hatching. Most small, newly hatched Atlantic croaker larvae were collected approximately 100 km offshore. Although the onshore component of advective transport is small in comparison with the average alongshore component, the estimate of shoreward transport rate is reasonable when age of larvae is considered.

CONCLUSIONS— RECRUITMENT IMPLICATIONS

Across-shelf transport appears to be an order of magnitude smaller than alongshore advective transport in the northwestern Gulf shelf waters during winter and spring. Sciaenid larvae collected offshore in the study area, at midshelf and beyond, would probably be lost to the estuaries in western Louisiana. Those offshore larvae would be transported towards north Texas estuaries, or back to the east if they were far enough offshore, since there is evidence for an easterly counter current (Kelly et al. 1982; Cochrane and Kelly 1986).

Sand seatrout are common in west Louisiana estuaries (Herke et al. 1984) and were the most abundant sciaenid larvae collected in this study. They spawn, in general, more inshore (Fig. 1) than Atlantic croaker or spot. Conceivably, many of the sand seatrout collected in the study area inside the coastal boundary layer on the inner shelf would have recruited to Louisiana estuaries.

Still, large numbers of postlarval sciaenids, other than sand seatrout, enter the estuaries in west Louisiana each year. Atlantic croaker and spot were the 3rd and 21st most abundant fish, of 117 species collected, in the Calcasieu River Basin, the largest estuary in west Louisiana (Herke et al. 1984). However, the distribution and transport analyses indicate that most spot and Atlantic croaker larvae directly offshore at least would not have recruited to the Calcasieu Basin. Interpretation of these data suggests that the source of the sciaenid postlarvae shown to seasonally recruit to the Calcasieu estuaries must be east of the study area. Interpretation of data summarizing several years of northern Gulf shrimp-trawl collections suggests that, during the spawning season, a sufficient concentration of adults exists to the east of our study area (Darnell et al. 1983).

In the fall and winter, high concentrations of Atlantic croaker, and to a lesser extent spot, have been found between the 20 and 40 m depth contours (65 and 125 km offshore) in an area east of the sampling grid. The area and timing of high concentration coincides with the reported spawning location and period for both Atlantic croaker and spot. If indeed this concentration represents a spawning distribution, it would help explain why so few Atlantic croaker and spot larvae, relative to the number of juveniles seen in estuaries, were collected in this and previous Gulf of Mexico ichthyoplankton studies. Unless collections were made in or near the spawning area, single-station densities would be low as eggs and larvae were dispersed. Furthermore, this study demonstrates the need for understanding both biological (vertical distribution, age and growth, behavior, etc. of larvae) and physical (ocean currents, estuarine-shelf exchange, etc.) processes which may influence estuarine recruitment.

ACKNOWLEDGMENTS

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BEHAVIOR OF SOUTHERN RIGHT WHALES, *EUBALAENA AUSTRALIS*, FEEDING ON THE ANTARCTIC KRILL, *EUPHAUSIA SUPERBA*

WILLIAM M. HAMNER,[1] GREGORY S. STONE,[2] AND BRYAN S. OBST[1]

ABSTRACT

Southern right whales, *Eubalaena australis*, were observed in 3 successive years on the western side of the Antarctic Peninsula. These whales do not appear to be from the well-documented Valdes, Argentina population. The whales we observed were feeding on Antarctic krill, *Euphausia superba*. When krill were at the surface right whales surface-skimmed at high speed, with upper jaw lifted above the water surface. In heavy weather one right whale "tail-sailed" at slow speed, with head submerged and apparently feeding. When krill were organized in subsurface schools, right whales engaged in subsurface feeding, diving repeatedly in place, apparently working a given school. One whale swam directionally to the only known large school of krill in the area and fed intensively, rested on the surface, then began a second feeding bout. Whales hyperventilated, false fluked, and fluked prior to feeding dives. These are the first detailed observations of feeding behavior of right whales in Antarctic waters and suggest that coastal Antarctica may have been (and may become again) a regular part of the summer feeding range of the species.

Right whales are among the rarest of the great whales, having been hunted almost to extinction a century ago. The southern right whale, *Eubalaena australis*, has been studied only recently and only during the austral winter when the whales aggregate inshore to bear calves and to mate (Clarke 1965; Payne 1976, 1986; Best 1981; Aguayo and Torres 1986). Because right whales were commercially extinct by the mid-1850's, very little has been learned about their ecology from the 20th century whaling industry. Information on feeding, migration, stock structure, and reproductive biology was collected for most other Antarctic mysticete whales during the heyday of whaling in this century (e.g., Mackintosh 1965; International Whaling Commission reports 1964-present). The small number of surviving right whales (ca. 2% of historic levels in the Southern Hemisphere, Breiwick and Braham 1984) has made it difficult for researchers to study this species. Our current understanding of its feeding and calving ecology in the Southern Hemisphere comes from observations made primarily off Peninsula Valdes, Argentina (Payne 1986).

In Antarctic waters south of lat. 60°S, more than 30 sightings of right whales have been reported previously (Berzin and Vladimirov 1981; Goodall and Galeazzi 1986; Ohsumi and Kasamatsu 1986). Most were in the vicinity of the South Orkney Islands, 9 were near the Antarctic Peninsula, 6 were in the Pacific sector of the Antarctic, and 2 were south of Africa. We have observed southern right whales during 3 consecutive austral summers near the western shore of the Antarctic Peninsula, and the sightings reported herein and in Stone and Hamner (in press) are the most southerly as well as the most detailed observations.

We sighted one individual during the 1983–84 austral summer (also recorded by Captain P. Lenie in the log of the RV *Hero*; Goodall and Galeazzi 1986), two individuals in 1984–85, and eight in 1985–86, four of which we individually identified. In 1986 a fortunate combination of fair weather and available ship time permitted us to make the first extended uninterrupted observations on the behavior of right whales feeding on the Antarctic krill, *Euphausia superba*.

METHODS

Right whales are distinguished by the absence of a dorsal fin and regions of cornified skin (callosities) on the head, jaws, and chin. Individual whales were identified by standard methods, using video tapes and telephotographs of head callosities and scarring patterns on the head and back (Payne et al. 1983; Kraus et al. 1986). When possible, we dropped large disks of plywood of

[1]Department of Biology, University of California, Los Angeles, CA 90024.
[2]College of the Atlantic, Bar Harbor, ME 04609.

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known diameter next to the whale and included it in the photograph to measure whale size.

Behavioral patterns were observed from the ship's bridge and recorded on a portable computer as they occurred, using a program which timed entries of encoded behaviors or coments to the nearest second. Krill schools were recorded on a Simrad echosounder and the identity of the organisms causing the echograms was verified by net samples taken with an Isaacs-Kidd midwater trawl and by divers' visual confirmation of krill schools near the surface.

RESULTS

7 January 1984: At 0500 hour, north of Cape Murray near Two Hummock Island, one right whale was feeding at the surface with its upper jaw lifted above the water, swimming at high speed (estimated at 8–9 knots by the ship's captain) in feeding runs of 15–20 seconds, which we recorded on video. Three humpback whales nearby were diving in one specific location. The right whale repeatedly changed direction between surface runs so that its horizontal directional feeding excursions did not take it far from the vicinity of the vertically diving humpbacks. During these powerful filter-feeding runs enormous amounts of water were displaced, cascading beside and behind the right whale and producing a large wake.

15 January 1985: A cow and a calf were swimming slowly at the surface some 500 m from the eastern shore of Anvers Island. On approach by the ship the whales swam slowly into shallow water where we could not follow. It was near dusk and we could not get photographs for future identification.

7 January 1986: We encountered one southern right whale and six humpbacks at 1830 hour at lat. 63°46′S, long. 61°13′W, between Trinity and Hoseason Islands. We photographed the head and body of the right whale for subsequent identification. We followed the whale for approximately 2 hours, recording diving times, surface intervals, and breathing rates. The whale frequently changed directions underwater and consequently we often failed to see the whale immediately when it resurfaced, so breathing rate data for this behavioral sequence are incomplete. The whale appeared to have captured krill on at least one dive because when the whale surfaced it repeatedly and briefly opened and closed its mouth, with baleen visible, a behavior presumably associated with separation of krill and water prior to swallowing the prey (Watkins and Shevill 1976). About 50 cape petrels, *Daption capensis*, alighted on the water and fed at the surface around the whale. When the whale's jaw movements ceased, the birds soon stopped feeding, but they remained on the water and did not follow the whale when it swam away at the surface.

2 March 1986: We observed one right whale at the northern end of the Neumayer Channel, where a large iceberg was grounded on a 93-fathom rise 2 miles east of Iceberg Point. The wind was blowing from the north at 20-24 knots and a strong surface current was flowing south, producing a bow wave on the grounded iceberg. The right whale repeatedly swam NE of the berg, raised its tail high out of the water at 90° to the wind, submerged its head, and "sailed" downwind past the iceberg, a behavior previously noted for right whales in Argentina (Payne 1976). Soon after we first saw the whale, it stopped tail-sailing and began diving, still along the N-S transect near the iceberg where it had been sailing. The presence of the ship did not cause the whale to alter its back-and-forth swimming rhythm or direction. We waited until the whale began one of its N-S transects past the iceberg and followed about 100 m behind it with the ship. A large school of krill was present on the east side of the iceberg. We recorded no other schools in the vicinity. The whale was accompanied by three female fur seals. The seals constantly darted about the head of the whale when it surfaced after long dives and appeared to annoy the whale, because several times the whale repeatedly slashed its head sideways when the seals swam too close.

3 March 1986: At 1030 hour, we spotted a single southern right whale near the mouth of Andvord Bay on the Antarctic Peninsula. The whale was swimming SSW at about 3 knots, making short dives that lasted about 19 seconds ($N = 12$, SD = 9.0 seconds), with brief surface intervals that averaged 6.1 seconds ($N = 12$, SD = 2.6 seconds) (Fig. 1). The whale then stopped diving but continued to swim SSW toward the NE tip of Lemaire Island, swimming mostly at the surface for approximately 90 minutes. During this period the whale appeared unconcerned with the ship, which remained 50–100 m behind it, but when the whale neared an iceberg that was hard aground near Lemaire Island, it turned suddenly at a right angle to its prior course and swam between the iceberg and the rocks. The ship was nonetheless able to follow the whale through the

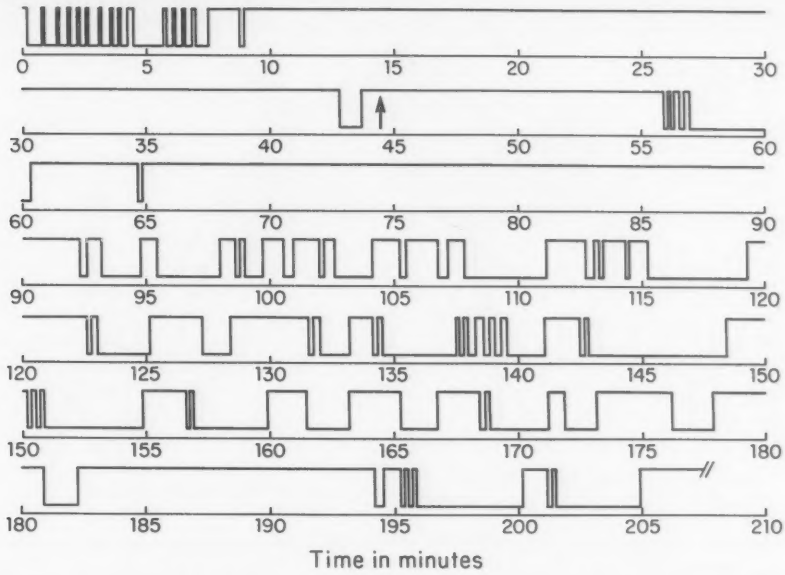

FIGURE 1.—Dive record of the right whale constantly observed for 3.5 hours on 3 March 1986. 44 minutes (arrow): The ship approached to within 10 m of the whale for i.d. photographs and size measurement. 54 minutes: The whale hyperventilated and dove in an area without krill, then swam northward. 92 minutes: The whale began diving on scattered small krill schools while still traveling N and NNW. 140 minutes: The whale stopped and began diving on one large concentration of krill. 182 minutes: The whale rested on the surface, moving its jaws. 194 minutes: The whale began a second feeding bout ca. 400 m further south.

narrow channel. Thereafter the whale ignored the ship and altered course to NNW, still swimming at the surface. The ship pulled ahead of the whale to measure its length and this may have caused the short dive noted at $t = 43$ minutes. However, the whale calmly surfaced again within 10 m of the ship and watched us while we photographed it next to the wooden disk. The whale was 11 m long. The whale then continued to swim at the surface to the NNW. During the period that the whale swam at the surface without diving the average time between breaths was 50.8 seconds ($n = 55$; SD = 10.8). At $t = 54$ minutes the whale began to hyperventilate, took three short dives, lifted the flukes partially clear of the water (false fluking) on the third dive, and then fully raised the flukes on the fourth dive, which lasted 210 seconds. The whale then remained at the surface for about 30 minutes while swimming northward.

This pattern of hyperventilation prior to a long dive occurred before every long dive sequence which was preceded by a surface interval of at least 4 minutes (Fig. 2). We used this criterion to restrict our dive selection for this plot because there is some indication that there is also a brief recovery period involving hyperventilation after long dives. Of the last 19 breaths that were taken during the 90 seconds before the 5 long dives plotted in Figure 2, 18 were less than 30 seconds apart, with a mean interval of 15 seconds ($N = 19$, SD = 7.3). During the time preceding this 90-s hyperventilation period, the whale averaged 1 breath every 48 seconds ($N = 17$, SD = 12.4), not significantly different from the time of 50.8 seconds recorded between breaths during long surface intervals without dives. During hyperventilation, therefore, breathing rate increased by about 3×.

At $t = 92$ minutes we began to record scattered small krill schools on the echosounder and the whale began to dive erratically, with some reasonably long dives, but most quite short. Of 23 dives, 13 (56%) were shorter than 10 seconds; the time averaged for all dives was 75.3 seconds

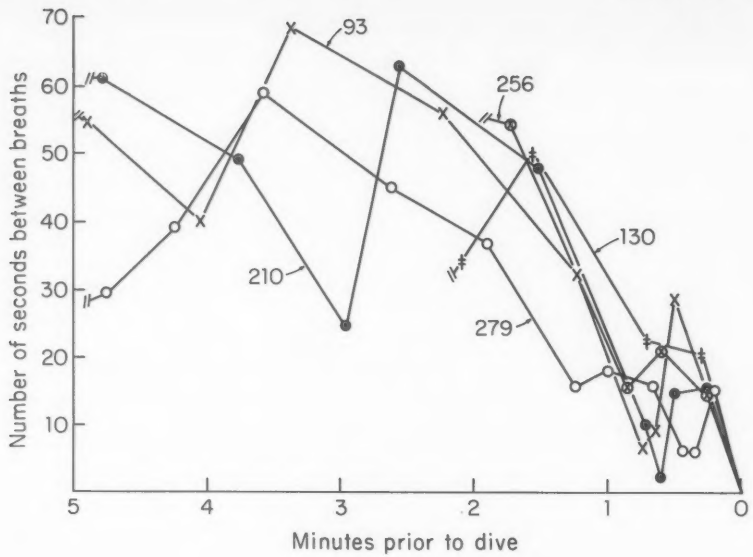

FIGURE 2.—Breath sequences prior to 5 dives lasting from 93 to 279 seconds. During the 90 seconds immediately preceding dives, the mean interbreath interval was 15 seconds. Prior to this 90-s period of hyperventilation the mean interbreath interval was 48 seconds.

($N = 20$, SD = 74.6). During this period of erratic diving the whale continued to swim N, then NNW. At about $t = 140$ minutes the whale stopped traveling NNW and began a series of 10 dives, the second being the longest, followed by successively shorter dives. These dives were followed by rather uniform surface intervals and all 10 lasted significantly longer ($\bar{x} = 183.5$ seconds, $N = 10$, SD = 89.2) than the previous mean of 75 seconds. At the end of the dive sequence, at 182 minutes, the whale stopped swimming entirely and floated motionless at the surface, occasionally moving its jaws. This inactivity lasted about 12 minutes and then the whale began a second series of dives. We called these dive sequences, which consisted of regular length surface intervals interspersed with a series of longer dives of progressively decreasing duration, "feeding bouts" because at $t = 140$ seconds the whale had reached the only major aggregation of krill in the vicinity, as verified by sonic records (Fig. 3). We saw dense schools of krill and isolated krill at the surface from the bow of the ship, and we captured krill in three successive hauls with the 1 m Isaacs-Kidd midwater trawl.

During the first feeding bout the whale slowed from its steady 3-knot swimming speed and moved slowly at about 1 knot, but no longer in any specific direction, finally swimming some 400 m to the south before beginning the second feeding bout. The whale had fed on krill earlier also, because it defecated during the feeding sequence and the feces, as determined by later microscopic examination, were composed entirely of well-digested euphausiids.

The display of a false fluke prior to the high fluke initiating a long dive did not necessarily indicate presence or absence of krill, but when krill were present, it was a highly significant predictor of the length of the dive. In the presence of prey, when the whale showed its flukes once (i.e., did not false-fluke preceding the dive), dive duration averaged 91.2 ± 13.0 seconds ($N = 5$), whereas when both a false fluke and a high fluke preceded the dive, the dive averaged 234.7 ± 64.4 seconds ($N = 7$).

In March and April 1986 we saw a total of eight southern right whales. Of these we distinguished four as individuals on the basis of video tapes and photographs of callosities and body markings. One of these whales was the same individual that we had observed in January some 70 miles fur-

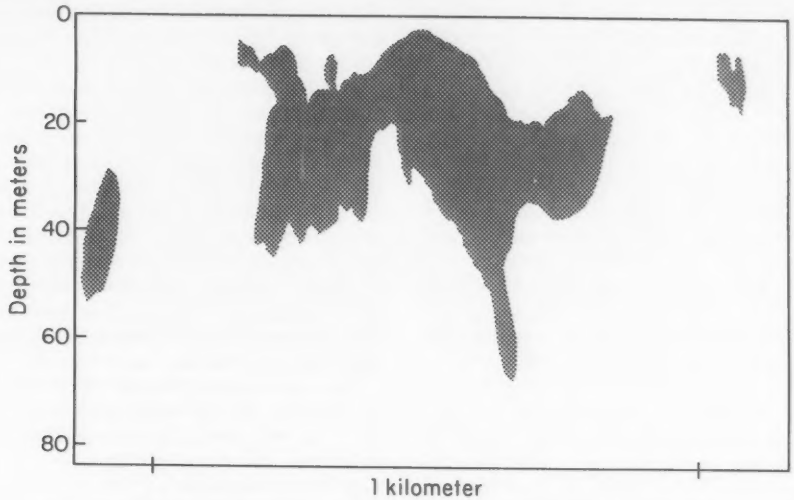

FIGURE 3.—Echogram of krill school on 3 March 1986 on which right whale stopped swimming and began feeding bout.

ther north, as confirmed by comparing video recordings of both sightings. Photographs of these four individuals were subsequently compared with the catalog of southern right whales that overwinter near Peninsula Valdes, Argentina (Payne and Rowntree 1984), but none of the Antarctic individuals were in that compendium of some 623 individuals.

DISCUSSION

Our observations of southern right whales along the Antarctic Peninsula suggest that coastal Antarctica may have been (and may well become again) a regular part of the summer feeding range of the species. These sightings indicate a more extensive distribution in the Southern Ocean than heretofore reported, an extension corroborated by the comparison of recent and historic summer distributional patterns by Ohsumi and Kasamatsu (1986). Southern right whales were hunted almost to extinction in the shallow coastal embayments where they overwinter more than 100 years before whaling began in the Southern Ocean (Harmer 1928; Townsend 1935). It is not surprising, therefore, that there are only a few scattered records of southern rights in Antarctic waters, fluke observations so to speak. During the past 50 years southern rights have been protected, and several demes of southern right whales have increased (Best 1981; Ohsumi and Kasamatsu 1986; Whitehead et al. 1986), and a commensurate extension of the summer feeding range into areas formerly occupied by these whales may be occurring.

It is interesting that none of the 4 individual whales for which we have photographic identifications appear in the catalog of 623 individual southern rights for the Valdes, Argentina breeding population (Payne and Rowntree 1984). We believe that the right whales we encountered in Antarctic waters probably winter elsewhere, perhaps along the Chilean coast, which has been less well surveyed than has the east coast of South America (Cardenas et al. 1986).

Payne (1976) described tail-sailing among the Valdes population of southern right whales and suggested that this may be a form of play behavior. In Antarctic waters this behavior may be a method used to forage on krill. The right whale that we observed tail-sailing had three fur seals in attendance, constantly darting about its head, apparently feeding on the same prey as the whale. Furthermore, tail-sailing occurred next to a grounded iceberg at a specific location that was repeatedly transected by the whale, the only spot in the vicinity where krill were detected on the ship's sonar.

Northern right whales feed by both surface-skimming and subsurface feeding, apparently holding the jaws agape below the surface much like they do when at the surface (Watkins and Schevill 1976, 1979). Surface-skimming by northern right whales that feed on copepods and juvenile euphausiids occurs at speeds of about 3 knots with relatively little turbulence (Watkins and Schevill 1976, 1979). The one southern right whale which we observed surface-skimming, and which was also mentioned in Goodall and Galeazzi (1986), swam at about 8 knots, with an immense amount of turbulence. This whale undoubtedly was feeding on *Euphausia superba*. The extremely high speed of this whale when surface-skimming may be related to type of prey. *Euphausia superba* is a large euphausiid that swims up to 30 cm/second, and it is quite adept at avoiding scuba divers and other dark objects (Hamner et al. 1983; Hamner 1984). It may be that right whales adjust the speed of their surface feeding runs to overcome the swimming speed of the particular prey that they pursue. Fin whales also exhibit differences in breathing and diving rhythms when feeding on euphausiids and on schooled fish (Watkins et al. 1984).

The southern right for which we have a 3.5-h record in 1986 fed exclusively below the surface. It swam for about an hour at the surface almost directly NNW toward the only patch of krill that we had located previously via the echo sounder during repeated transects across the mouth of Andvord Bay. It is not understood how baleen whales locate prey. They might echolocate, they might listen for krill noises, or they might remember where they had prior success and return to the general vicinity and then begin to hunt randomly. Although our data do not allow us to choose among these possibilities, it appears that this particular southern right whale did navigate directly to patches of prey, as suggested by Watkins and Schevill (1979) for northern right whales. However, some subsurface searching probably occurs as well. The whale that we followed for the longest period of time made a reasonably long dive of 210 seconds in the middle of its surface swim toward the krill patch. It apparently did not find anything to eat (nor did the sonar indicate the presence of krill), and it made no more significant dives for about 30 minutes.

When the whale reached an area with small scattered krill schools, its dives were generally short, and the temporal spacing and duration of dives and surface intervals were erratic. When the whale reached a large school of krill it stopped swimming between dives, dives lasted longer, surface intervals between dives became more regular, and successive dives were progressively shorter. After 10 of these dives the whale floated without any swimming movements at the surface for about 12 minutes while occasionally rattling its baleen and slightly lifting its upper jaw.

The whale clearly anticipated its dives. It hyperventilated for about 90 seconds prior to all of the long dives. Hyperventilation is a common precursor to diving in air-breathing vertebrates (Kooyman et al. 1981), but this respiratory pattern apparently has not been reported previously for a baleen whale.

The data that we present in support of this feeding pattern are admittedly modest, consisting of only one continuous 3.5-h data sequence for one individual. Nonetheless, this data set is truly unique and it includes a series of statistically significant changes of behavior at the surface and at depth which are correlated with prey distribution. Since the changes of behavior are real, they merit interpretation. One hypothesis to account for the increase and then the decrease in dive length after encountering prey is that the whale dove to its full capacity in order to maximally exploit an opportunity to feed. With repeated dives its dive capacity may have diminished, producing first long, then shorter and shorter dives (Fig. 1). In contrast, this breathing pattern has not been observed in grey whales, which exhibit a sustained capacity for repetitive, nearly monotonic diving while feeding (Obst et al. in prep.). It is possible that right whales, being more specialized for surface-skimming, become exhausted more readily during sustained diving.

An alternative hypothesis to account for this pattern of behavior is that the whale captured krill with such ease on the first long dive of 348 seconds that a "digestive bottleneck" (Kenward and Sibly 1977) developed; subsequent dives would be progressively shorter because the stomach (or some storage chamber) filled more rapidly than the food could be processed. The long surface interval of immobility followed by a second feeding bout might then represent the time taken to clear such a chamber (e.g., the first of the three stomach pouches) in preparation for the next bout of feeding. If this hypothesis is correct, it implies that once a right whale has found a particularly favorable school of krill, it fills up very rapidly. This interpretation contrasts markedly with a popular impression of great whales as continuous

feeders that harvest prey while swimming lazily through diffuse planktonic resources. Herwig et al. (1984) presented preliminary evidence that microbial fermentation of ingesta may occur in the forestomach of baleen whales, a process which may be expected to limit the throughput rate of food in accordance with continuous-flow, stirred tank reactor kinetics (Penry and Jumars 1987). It is tempting to speculate that the feeding behavior of right whales, among the largest endotherms on earth, may be constrained by a digestive bottleneck analogous to that described for hummingbirds (Karasov et al. 1986), the smallest of endotherms. These hypotheses warrant subsequent testing through more extensive time-budget analyses of right whales and other balaenopterans on their feeding grounds, such as described here and in Watkins et al. (1984).

ACKNOWLEDGMENTS

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NOTES

AN ECONOMETRIC ANALYSIS OF NET INVESTMENT IN GULF SHRIMP FISHING VESSELS[1]

The major capital inputs in the Gulf shrimp fishery are vessels and gear. Early vessels, built mostly of wood, employed drag seines, cast nets, and fixed traps to catch shrimp. Today, much larger and more powerful vessels, equipped with sophisticated fishing gear and accessories, trawl the Gulf of Mexico. The last 20 years has seen a remarkable substitution of steel and fiberglass vessels for wooden vessels. The factors underlying this aggregate investment trend in the Gulf of Mexico (hereafter referred as the Gulf) shrimp fishery, however, have yet to be examined.

Economic analysis of the fishing industry has increased in recent years because of the growing importance of world fish stocks. However, these studies have been focused predominantly at the micro or firm level (Thompson et al. 1970[2]; Wilson et al. 1970; Juhl 1974; Watson 1977; Griffin et al. 1978; Prochaska and Cato 1981). Moreover, accounting for a comprehensive mean of the cost of capital has been ignored in past research efforts. Yet, the cost of capital is likely a major factor in fishing vessel investment decisions in the Gulf shrimp fishery. The long run profitability of the sector and its exposure to financial risk depends, to a large extent, upon its capital structure and fluctuations in the cost of debt and equity capital. Futhermore, this determinent of aggregate investment behavior represents a major channel through which macroeconomic policy actions are transmitted to the Gulf shrimp fishery.

The purpose of this study is to estimate an econometric model of annual real net investment in fishing vessels in the Gulf and to determine the sensitivity of investment decisions in the industry to fluctuations in the cost of equity and debt capital. This study begins by examining the individual factors that affect the expansion of the stock of steel, wood, and fiberglass vessels in the Gulf fleet. The effects of alternative macroeconomic policies on investment expenditure trends in the Gulf shrimp fishery are then studied. The final section of this paper presents some concluding remarks.

Determinants of Net Investment

The aggregate investment model used in this study is based upon the neoclassical theory of aggregate investment behavior. The determinants of the desired capital stock of fishing vessels as well as the relationship between this desired capital stock and net investment behavior of Gulf shrimp fishermen are specified in this section.

Desired Stock of Fishing Vessels

In making investment decisions, competitive firms add to their existing stock of capital as long as the present value of the periodic net cash flows generated by an additional unit of capital exceeds its net purchase price. This condition for any particular type of fishing vessel (e.g., wood, steel, fiberglass) can be stated algebraically as follows[3]:

$$\sum_{t=1}^{\infty} p(\partial X/\partial K_j) - (\partial T_t/\partial K_j) - r(\partial D_t/\partial K_j)$$

$$- (\partial P_t/\partial K_j)(1+\rho)^{-t} > q_j(\alpha - i_c)$$

$$\times \left(1 + \sum_{t=1}^{\infty} \partial R_{jt}/\partial K_j\right)(1+\rho)^{-t}\Big) \qquad (1)$$

where variable p represents the real price fishermen expect to receive per unit of output in the Gulf of Mexico shrimp industry, X represents the quantity of shrimp expected to be harvested, K_j is the real stock of the j^{th} category of fishing vessels, T_t and P_t represent the tax payment and principal payment due in period t expressed in constant

[1]Technical Article No. TA-20803 of the Texas Agricultural Experiment Station, Texas A&M University System. This research was supported in part by the Texas A&M University Sea Grant College Program under Grant No. NA81AA-D-00092.

[2]Thompson, Russel G., R. W. Callen, and L. C. Wolken. 1970. Optimal investment and financial decisions for a model shrimp fishery firm. Unpubl. Rep. Texas A&M Univ., TAMU-SG-70-205.

[3]The variables without any subscripts are expected at the time the investment is made to remain constant over time.

dollars, D_t represents debt outstanding in period t, r is the real rate of interest on debt capital, ρ is the real after-tax opportunity rate of return on equity capital desired by fishermen, q_j is the real price paid for the j^{th} category of fishing vessels at the retail level, α is the proportion of investment financed with equity capital, i_c is the investment tax credit rate, and R_{jt} represents the real level of replacement investment in the j^{th} category of fishing vessels required in period t to offset losses in productive capacity due to wearout.

The entire term on the left-hand side of the inequality sign in Equation (1) represents the present value of the additional net cash flows generated by a permanent addition to the j^{th} category of fishing vessels. It is assumed that both the interest and the principal payments, $(\partial P/\partial K_j)$ and $r(\partial D/\partial K_j)$, vary over time as further expenditures are required to maintain the productive capacity of this addition to the capital stock at its original level. The right-hand side of Equation (1) represents the initial downpayment minus the investment tax credit plus the present value of all future cash outlays required to maintain the stock of the j^{th} category of fishing vessels at its new level.

To maximize the present value of their equity, Gulf shrimp fishermen would continue to add to the stock of the j^{th} category of fishing vessels until Equation (1) holds as an equality. Equivalently, maximization of the present value of owner equity requires that[4]

$$p(\partial X/\partial K_j) = \frac{q_j \rho}{(1 - F_j)} \cdot \frac{\alpha - i_c + Z - A}{(1 - i_Y)} \qquad (2)$$

where F_j represents the present value of the stream of capacity depreciation of the j^{th} category of vessels and i_Y is the average income tax rate. The term Z represents the present value of the stream of after-tax interest payments and principal payments on debt while A represents the present value of the stream of tax depreciation allowances that can be claimed for each dollar of investment as the stock of vessels is maintained at its new level.[5] The right-hand side of this expression thus represents the implicit rental price of the j^{th} category of fishing vessels.

The concept of the implicit rental price of capital has been widely employed in previous studies of investment behavior as a determinant of the capital stock which firms desire to hold (e.g., Coen 1968, 1975; Penson et al. 1981). Equation (2) suggests that the implicit rental price of the j^{th} category of fishing vessels will increase if their purchase price, the cost of debt, and equity capital, or income tax rates increase. These effects, however, will be offset to some extent by an increase in the investment tax credit rate, the deductibility of tax depreciation allowances, and interest expenses.

Let us assume that output in this industry is a function, in part, of the stock of fishing vessels and that this production relationship is of the Cobb-Douglas form. Letting β_j represent the partial production elasticity associated with the stock of the j^{th} category of fishing vessels (K_j), the marginal physical product for these vessels can be expressed as follows:

$$(\partial X/\partial K_j) = (\beta_j(X/K_j). \qquad (3)$$

Substituting Equation (3) into Equation (2), the desired stock of the j^{th} category of fishing vessels at the end of year t can be expressed as follows:

$$K^*_{jt} = \beta_j(pX/c_j)_t \qquad (4)$$

where c_j represents the expected implicit rental price of the j^{th} category of fishing vessels given by the right-hand of Equation (2). Equation (4) implies that the desired stock of j^{th} category of fishing vessels is directly related to the expected real gross income from Gulf shrimp fishing and is in-

[4]Equation (1) as well as the derivation of the implicit rental price of vessels (c) assume that fishermen expect real prices (p) and the marginal physical product of vessels $\partial X/\partial K$ to remain at current levels. These and other assumptions which allow us to treat many components of Equation (1) as consoles are consistent with those employed in Penson et al. (1981) and Coen (1975).

[5]The nominal value of Z (the present value of the stream of after-tax loan payments) in Equation (2) is equal to

$$(1 - i_Y)\Psi \sum_{i=1}^{n} d_i(1 + \phi)^{-i}(1 + \rho)^{-i}$$

$$+ \Psi \sum_{i=1}^{n} (e - d_i)(1 + \phi)^{-i}(1 + \rho)^{-i}$$

while the real value of A (the present value of the stream of depreciation allowances is equal to

$$i_Y(\delta/(\rho + \phi + \rho\phi + \delta))$$

where d_i is equal to the nominal interest payment on a loan of one constant dollar, ϕ is the inflation rate, e is the nominal amortized loan payment on a loan of one current dollar, and δ is the tax depreciation rate given by $2/n$ where n is the service life of the vessel.

versely related to the expected implicit rental price of these vessels. Similar equations could be developed for other inputs used in the shrimp fishing effort.

Desired Net Investment in Fishing Vessels

New fishing vessels are acquired by Gulf shrimp fishermen both to expand their productive capacity and to replace losses in the productive capacity of existing vessels. This partitioning of observed gross investment into net investment and replacement investment for the j^{th} category of fishing vessels can be expressed definitionally as follows:

$$N_{jt} = K_{jt} - K_{jt} = I_{jt} - R_{jt} \tag{5}$$

where I_{jt} represents the level of real gross investment in the j^{th} category of fishing vessels in year t while R_t is the real replacement investment needed to offset annual capacity depreciation of these vessels. The variables K_t and K_{t-1} represent the productive capital stock of the j^{th} category of fishing vessels the end and the beginning of the year, respectively. Given Equations (4) and (5), the following relationship between the desired stock of the j^{th} category of fishing vessels and current real net investment in these durable inputs can be defined:

$$N_{jt} = \theta_j(K^*_{jt} - K_{jt-1}) \tag{6}$$

where $0 < \theta_j \leq 1$ and where θ_j represents the partial adjustment coefficient that describes the speed of adjustment of actual stocks to desired levels for the j^{th} category of fishing vessels. Substituting Equation (4) into Equation (6) and assuming an adaptive expectations hypothesis for $(pX/c_j)_t$, the following compound geometric expression is obtained:

$$N_{jt} = \theta_j\,\beta_j\lambda(pX/c_j)_t + (1-\lambda_j)N_{jt-1} + \theta_j(1-\lambda_j)K_{jt-2} - \theta_j K_{jt-1} + \mu_{jt} \tag{7}$$

where λ_j is the adaptive expectations coefficient and μ_{jt} represents the error term. Since K_{jt-2} is equal to $K_{jt-1} - N_{t-1}$, Equation (7) reduces to the following estimating equation:

$$N_{jt} = b_{j0} + b_{j1}\,(pX/c_j)_t + b_{j2}\,K_{jt-1} + b_{j3}\,N_{jt-1} + \mu_{jt} \tag{8}$$

where b_0 is the intercept, $b_1 = \theta\ \beta\lambda$, $b_2 = -\theta\lambda$, $b_3 = (1-\lambda)\ (1-\theta)$ and μ_t is once again the random disturbance term. The estimates of the b_1 and b_3 coefficients are expected to be positive while the value of b_2 is expected to be negative.[6] Equation (8) thus represents the general form of the equations to be econometrically investigated in this study.

Data

The time series data used in this study consist of annual observations for each variable in Equation (8) over the 1965-77 period. This time period represents the only period for which investment expenditure information is available.

The productive capital stock of the j^{th} category of fishing vessels is comprised of a series of different vintages of vessels or

$$K_{jt} = I_{jt} + (1-h_{j1})I_{jt-1} + (1-h_{j1}-h_{j2})I_{jt-2} + \ldots + (1-h_{j1}-h_{j2}-\ldots-h_{jn})I_{jt-n} \tag{9}$$

where h_{ji} is the fraction of the j^{th} category of fishing vessel's original productive capacity lost in the i^{th} year of its service life. The value of h_i is represented by $(1-\phi)^{i-1}$, where $\phi = 2/n$ and n is the assumed service life.[7] In a related matter, the present value of the stream of capacity depreciation of a vessel (F_j) was computed as follows:

[6]The net investment model expressed in Equation (8) can be seen as a part of a simultaneous equation system that includes other investment equations as well as supply equations for all inputs and the production function for the fishing industry. The specification of the complete simultaneous system of equations and measurement of time series data needed to simultaneously estimate the b_i coefficients in Equation (8) are beyond the scope of this study. Since the disturbance terms for this set of investment equations are likely correlated, the seemingly unrelated regression equations estimator was employed. The disturbance terms given by this estimator were also examined for autocorrelation. The estimated rho coefficient in this small sample was shown to be insignificant in all cases. Finally, the predicted rather than actual value of N_{t-1} was used in estimating Equation (8) to address the possibility of correlation between the lagged dependent variable and the disturbance term.

[7]While a geometric decline in productive capacity has been assumed for fishing vessels, recent studies indicate that the productive capacity of equipment and machinery deteriorates at a lower rate in the early period than in latter years. Coen (1975) suggested that equipment and machinery deteriorate as they age, though not necessarily at a geometric rate. For farm tractors, a concave decay pattern represents the best proxy for the capacity depreciation pattern suggested by engineering considerations (Penson et al. 1981). The true pattern which underlines actual capital spending decisions in the fishing industry could not be examined due to inadequate data.

$$F_j = \sum_{i=1}^{\infty} h_{ji}(1 + \rho)^{-i} \qquad (10)$$

Data from the National Marine Fisheries Service were used as annual observations on the nominal value of gross investment in Gulf fishing vessels (U.S. Department of Commerce 1965-77[8]). These values were deflated to real terms using the industrial price index. The quality of the time series for real net investment in fishing vessels, N_t, depends on how well the annual values of I_t reflect quality changes in vessels over time.

The annual levels of the implicit rental price of vessels (c) were computed using the definition outlined on the right-hand side of Equation (2). Coen (1975) assumed that the real after-tax rate of return desired on equity capital, ρ, is constant over the economic life of the investment. Following the lead of Coen, a value for ρ of 5% was employed in this study.

The real rate of interest on nonreal estate loans at commercial banks, r, along with annual rate of inflation equals the nominal rate of interest on debt capital. Annual values for all these variables were obtained from U.S. Department of Commerce publications. The annual values for the fraction of investment expenditures that are debt financed (ψ) used in computing Z were found by dividing the annual change in total debt in the fishing industry by the annual level of gross investment in durable inputs provided by the National Marine Fisheries Service. The time series for a, the fraction of capital expenditures financed with internal equity capital, was equal to one minus the percentage debt financed $(1 - \psi)$.

Investment tax credit rate, i_c, was equal to 7% during the 1965-68 period, 0% during the 1969-70 period, and 10% during the 1971-77 period. The maximum corporate income tax was assumed to represent i_y for the Gulf shrimp fishery. The double-declining balance method was assumed in determining the present value of the stream of annual tax depreciation allowances in A.

The time series data on prices paid for vessels, a component of the rental price, were measured using cost data collected from shrimp vessel builders. Griffin et al. (1978) have shown that vessel length, material of construction, and year of purchase were the most significant factors determining the price of a vessel. The equation estimated in that study was used to extend available vessel price information over the entire time period covered by this study.

[8]U.S. Department of Commerce. 1965-77. Vessel characteristics data. National Marine Fisheries Service, NOAA, Wash., D.C.

Econometric Results

Statistical as well as economic criteria can be employed to evaluate the estimated equations for the various categories of fishing vessels. The economic criteria include the reasonableness of the elasticities for the economic variables and as well the partial production elasticities implied for the production function.

Empirical estimates of the annual real net investment model for steel, wooden, and fiberglass vessels indicate statistically significant coefficients for all but one of the explanatory variables at the 10% level or less (Table 1). The lone exception was the coefficient associated with the lagged capital stock variable in wooden vessel model, which was not significantly different from zero at less than the 20% level. All the coefficients associated with the explanatory variables have the signs hypothesized earlier in this paper. Finally, the coefficients on the lagged dependent variable satisfy the constraint of being both greater than zero and less than one.

TABLE 1.—Estimated coefficients for the annual net investment model for fishing vessels. Gulf Shrimp Fleet, 1965-77.

Vessel type	Constant (b_0)	$(pX/c)_t$ (b_1)	K_{t-1} (b_2)	N_{t-1} (b_3)
Steel	−95.3895	4.3770	−9.1302	0.6318
		[1](6.21)	(6.23)	(2.34)
Wooden	384.3848	0.1132	−3.1944	0.9089
		(1.79)	(0.93)	(1.21)
Fiberglass	0.3819	0.2990	−0.9529	0.2765
		(5.37)	(1.74)	(2.88)

[1]Numbers in parentheses indicate absolute values of t-statistic.

Economic criteria employed in evaluating the reasonableness of the empirical results and in comparing the investment behavior among vessel types include the partial production elasticity of fishing vessels (β). This elasticity is given by $-b_1/b_2$ which is computed using the estimated beta coefficients in Equation (7). It appears that steel vessels, with a partial production elasticity of 0.479, are highly productive and play an important role in the supply of fish. The fishing sector, unlike other sectors of the economy, depends pri-

marily on one major capital input—vessels. Therefore, the high partial production elasticities recorded for steel vessels and fiberglass vessels (0.314) are no surprise. Even though wooden vessels appear to incur more repair and maintenance costs, attract a lower quality crew, and, for that matter, are less efficient than the other vessel types, the low partial production elasticity of 0.033 is surprising. This low partial production elasticity may have been caused by the fact that the instrument for N_{t-1} in the wooden vessels equation used to address the issue of the relationship between the lagged dependent variable and the error term did a poor job of explaining N_{t-1}.

An examination of the elasticities associated with the $(pX/c)_t$ term, computed at the mean, reveals that real net investment in steel vessels is the most sensitive to changes in prices, interest rates, taxes, and the other factors captured in this variable. An elasticity of 7.28 associated with this economic variable was computed for steel vessels. This means that a 1% change in the $(pX/c)_t$ variable causes real net investment in steel vessels to change by 7.28%. This high investment response to changes in these economic relationships could be attributed to the fact that steel vessels, by far the most productive (as evidenced by the high partial production elasticity reported earlier), are the most durable and the most capital intensive. The elasticity associated with the $(pX/c)_t$ term in the fiberglass and wooden vessel equations were 5.35 and 3.11, respectively. This would suggest that macroeconomic policy actions would have a substantially greater effect on real net investment in steel vessels than, say, wooden vessels.

Impact of Changes in Cost of Capital

The impact of high real interest rates on the growth of selected sectors in the economy has been of great concern in the 1980s. The sensitivity of annual real net investment in fishing vessels to changes in the real rate of interest is examined in this section by simulating the estimated equations under annual real rates of 5 and 10%. In the short run (3 years), an increase in the real rate of interest on debt capital from 5 to 10% would cause real net investment in fishing vessels to decrease by 3.04%. Annual real net investment in these fishing vessels would decrease by 15.88% in the long run. As the real rate of interest on debt capital increases, it becomes more difficult to justify the purchase of additional vessels owing to their rising marginal factor cost. Given the fact that 67% of the cost of new fishing vessels is normally financed with debt capital, it is not surprising that rising real interest rates on debt captial have a significant negative effect on the long run expansion of the Gulf fleet.

The real cost of equity capital, which reflects the opportunity cost of the fisherman's own funds, has a less dramatic effect on annual real net investment in fishing vessels. This can be attributed to the fact that only 33% of the cost of new fishing vessels are financed with equity capital. The short run impact of an increase in the real cost of equity capital from 5 to 10% translates into only a 1.76% decrease in annual real net investment in fishing vessels in the short run. This same change in the cost of equity capital would result in a 12.32% decrease in annual real net investment in the long run.

Summary and Conclusions

This study evaluated aggregate investment behavior by fishermen for steel, wooden, and fiberglass fishing vessels in the Gulf of Mexico shrimp fishery and examined the implications of changes in the cost of acquiring debt and equity capital on the industry's investment response. This study showed statistical justification for the theoretical model of aggregate investment behavior for all three vessel types.

It is quite evident that the cost of capital plays an important role in influencing the investment decisions in the Gulf shrimp fishing industry. Macroeconomic policies that lead to high real interest rates depress real net investment in this fishery. Capital expenditures for steel vessels are the most sensitive to changes in real interest rates while wooden vessels are the least sensitive. While low real interest rates are desirable for stimulating investment activities in the general economy, they would add to the overcapitalization problem which currently exists in the Gulf shrimp fishing industry. Finally, this study underscores the need to reinitiate efforts to collect data on gross investment expenditures for different categories of fishing vessels in the Gulf fleet.

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JOHN B. PENSON, JR.
ERNEST O. TETTY
WADE L. GRIFFIN

Department of Agricultural Economics
Texas A&M University
College Station, TX 77843-2124

APPENDAGE INJURY IN DUNGENESS CRABS, *CANCER MAGISTER*, IN SOUTHEASTERN ALASKA

The Dungeness crab, *Cancer magister*, is commercially important along the western coast of the United States. Like many decapod crustaceans, it can autotomize and regenerate appendages to heal wounds and limit injury.

Studies of appendage injury may be useful in assessing the physical condition of crustacean populations and the impact of fishing on commercially important species. Incidences of appendage loss in the field have been reported for species of crabs other than *C. magister* (McVean 1976; McVean and Findlay 1979; Needham 1953). Appendage loss was studied in adult Dungeness crabs in Washington (Cleaver 1949) and Oregon (Waldron 1958) and for juvenile crabs in the Columbia River estuary (Durkin et al. 1984).

In this study we examined adult Dungeness crabs in southeastern Alaska to determine the incidence of missing, regenerating, and damaged appendages. Temporal incidence of appendage injury was compared to the molting and mating periods of the crabs and to the commercial fishing season for Dungeness crabs.

Materials and Methods

Adult Dungeness crabs were collected from Icy Strait and the Excursion Inlet fjord near Glacier Bay, AK (lat. 135°30'N, long. 58°25'W), from May through November 1984-85. Data were obtained by monthly surveys of commercially caught crabs. Crab pots (Waldron 1958) were set at depths of 7 to 20 m and remained in the water for 3 to 11 days. All crabs were held in live tanks (<24 hours) before they were measured on board ship. In southeastern Alaska, pots are equipped with escape rings to permit release of crabs with carapace widths <165 mm, but sublegal-sized crabs are often found in the catch.

Carapace width (excluding the 10th anterolateral spines), wet weight, and sex were recorded for each crab. Carapace condition was graded as soft-shell (recent molt), new-shell, worn-shell, or skip-molt (Somerton and Macintosh 1983). The number and identities of missing, damaged, or regenerating chelipeds and walking legs were recorded. An appendage with a cracked cuticle or missing dactyl was considered damaged. Appendages smaller in length and diameter than intact appendages were designated regenerating. Combined missing, damaged, and regenerating appendages are referred to as injured appendages.

Interrelationships between variables were determined with Pearson correlations (SAS 1985). Means were compared with Student's t-tests, and chi-square analyses were used to determine if multiple autotomies occurred by chance (Steel and Torrie 1960). Data are presented as means ± 1 standard error of the mean.

Results

Males comprised 65% and females 35% of the 878 Dungeness crabs examined. Average carapace widths were 169 ± 0.6 and 159 ± 0.7 mm for males and females, respectively. Wet weights were $1{,}102 \pm 9$ g for males and 884 ± 14 g for females. The greatest number of female crabs was caught in July, and the greatest number of males in August.

Seventy-five percent of the crabs were intact, with no appendage injuries. Twenty-five percent of all crabs had injured limbs; 18% had missing, 5% had regenerating, and 2% had damaged appendages. No relationship existed between carapace width and appendage injury.

Most of the Dungeness crabs sampled were in the worn-shell condition (67%). Twenty-eight percent of all crabs were new-shelled. Only 1% were soft-shelled and 4% were skip-molts. Correlations between carapace condition and appendage injury were not significant.

No significant differences existed in appendage injury between male and female Dungeness crabs. Injuries were bilaterally symmetrical except for the 3d walking leg which was missing more frequently on the left side ($P < 0.05$). Considering only those crabs with missing legs, a total of 246 legs were missing with a mean of 1.5 ± 0.1 missing legs/crab. Ninety-seven crabs had legs missing on the right side and 98 had legs missing on the left side. The maximum number of missing legs per crab was 5. Sixty percent of the crabs had 1 leg missing, 20% had 2 missing legs, and 12% were missing 3 or more legs. Of the crabs with missing legs, 63% were males and 37% were females.

Forty Dungeness crabs had regenerating legs, with a mean of 1.2 ± 0.1 regenerating legs per crab. Sixty percent of those crabs had 1 regenerating leg, 10% had 2 regenerating legs, and 3% had 3 or more regenerating legs. The maximum number of regenerating legs per crab was 4. Of the crabs with regenerating legs, 73% were males and 27% were females.

Seventeen crabs had damaged appendages with a mean of 1.1 ± 0.1 damaged appendages/crab. Of the crabs with damaged appendages, 82% were males and 18% were females.

The observed number of Dungeness crabs with 2 or more missing appendages was significantly higher ($P < 0.01$) than expected for both sexes, indicating that appendage loss was not due only to chance.

Appendage injury was significantly correlated with date, with more injuries occurring later in the year. The number of Dungeness crabs with missing appendages was significantly correlated with date for both males and females ($P < 0.01$). The lowest percentage of crabs with injured appendages occurred in July (4.8%, both sexes combined) and increased to a maximum of 34.3% in November. The percentage of male crabs with regenerating appendages did not vary significantly over time and was about 6% for all months. However, the percentage of female crabs with regenerating legs increased from 0% in May to 10.5% in November ($P < 0.01$). Male crabs with damaged appendages increased from 0% to 8.5% from May to October ($P < 0.05$) and then decreased to 1.7% in November.

Chelipeds and 1st and 4th walking legs were injured most frequently. The hierarchy for frequency of injury for female crabs (chelipeds > 4th walking legs > 1st, 2d, and 3d walking legs) differed slightly from the hierarchy for males (chelipeds > 1st walking legs > 4th walking legs > 2d and 3d walking legs). Months in which high percentages of crabs had injured chelipeds also had high percentages with injured 1st (males) and 4th (females) walking legs (Fig. 1).

The temporal incidence of appendage injury in Dungeness crabs was compared to life history events and to the commercial crab fishing season in southeastern Alaska (Fig. 2). The season opened 15 June and closed 15 August, reopened 1 October and closed 28 February 1986. Appendage injuries were low in July and increased 157% from July to August, a period of simultaneous molting, mating, and fishing. An additional increase in appendage injury of 43% occurred in October, even though the fishery was closed from 16 August to 30 September.

Discussion

Pot samples are biased towards larger sized Dungeness crabs because of the size of the mesh on the pot and the presence of two escape rings with diameters of 11 cm. However, 62% of the crabs collected for this study were either male crabs with carapace widths <165 mm or were females. Very few soft-shell crabs were caught, even though molting was occurring during part of the sampling period. Our dependence on commercial crabbers for data collection restricted us to sampling mostly during the open fishing season when most of the crabs were not in the soft-shelled condition.

Twenty-five percent of the Dungeness crabs sampled in southeastern Alaska had appendage injuries. In other studies of Dungeness crabs in Washington, Oregon, and the Columbia River estuary, 18%, 32%, and 62%, respectively, of the crabs were injured (Cleaver 1949; Waldron 1958; Durkin et al. 1984). The crabs examined in our study were held for up to 24 hours in crowded tanks on board ship before being measured and

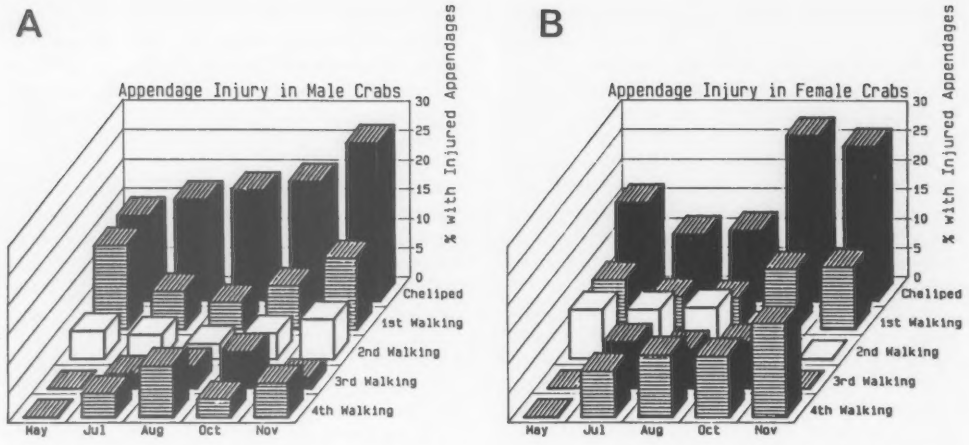

FIGURE 1.—Monthly percentages of male (A) and female (B) Dungeness crabs with injured (missing + regenerating + damaged) chelipeds and walking legs.

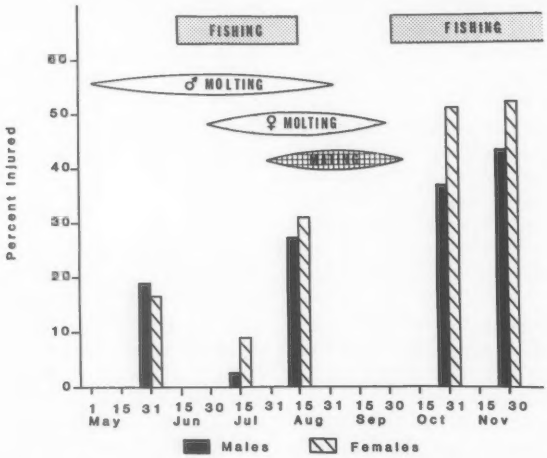

FIGURE 2.—Temporal relationships of percentages of male and female Dungeness crabs with injured (missing + regenerating + damaged) appendages to the crabs' molting and mating periods and the commercial crab fishing season in southeastern Alaska.

were sometimes observed grasping other crabs, but very few autotomized limbs were found in the tanks.

The estimate of appendage injury may be low if Dungeness crabs with injured appendages were less likely to enter pots than intact crabs. In another study, the observed number of *Carcinus maenas* missing 2 or more legs was higher than expected if multiple autotomies occurred by chance, which was interpreted to mean that injured *C. maenas* enter pots as readily as intact crabs (McVean 1976). Because there were more Dungeness crabs with 2 or more missing legs in our collections than would be expected if multiple

autotomies occurred by chance alone, our data could be similarly interpreted to suggest that Dungeness crabs with injured appendages showed little decrease in pot-entering ability and that our estimate of injury was accurate. For this interpretation of the chi-square results to be valid, one must assume that all injuries occurred before the crabs entered pots and that injury did not occur within the pots.

Appendage injury in Dungeness crabs was bilaterally symmetrical except for the 3d walking leg. Interestingly, Easton (1972) demonstrated that 3d walking legs of *Hemigrapsus oregonensis* were the most easily autotomized. In other studies, both bilateral symmetry and asymmetry have been reported for different species of crabs (Durkin et al. 1984; Needham 1953). Asymmetrical appendage loss has been associated with crabs that move predominantly in one direction, while symmetrical leg loss occurs in crabs that move randomly (Needham 1953).

The chelipeds, followed by the 1st and 4th walking legs, were most vulnerable to injury. Limb loss has been correlated in other studies with degree of exposure of the limb; the outermost limbs, the longest limbs and limbs with postures that afford little protection are most frequently lost (Needham 1953). Anterior limbs are lost more frequently than posterior limbs (Needham 1953). The chelipeds are the most anterior and one of the most exposed appendages on Dungeness crabs and are frequently used in aggressive threat postures. After loss of chelipeds, the 1st walking legs remain as the most anterior, exposed limbs and therefore, the most vulnerable. The 4th walking legs are the most posterior and also very exposed limbs on an intact crab.

A significantly greater number of Dungeness crabs with 2 or more missing legs was observed than expected if multiple autotomies occurred by chance, indicating an increased susceptibility to subsequent appendage loss after initial injury (Needham 1953; Easton 1972).

The correlations between appendage injury and date were significant but may not be biologically important. Although these correlations were significant, the r^2 values (square of the coefficient of variation) were low. Increased appendage injury later in the year may be related to other factors. Soak times, the length of time pots were left in the water, were longer later in the year. Dungeness crabs may cannibalize other crabs while confined in pots (Waldron 1958). There may also be delays between time of injury and subsequent autotomy and regeneration. Regeneration of legs in Dungeness crabs is usually completed after 2 or 3 molts (Cleaver 1949).

Over the sampling period, only 5% of all crabs had regenerating appendages while 18% had missing appendages. The discrepancy may be due to increased mortality of the crabs following injury (McVean and Findlay 1979), or by the efficient, yearly removal of legal-sized, injured crabs by the commercial fishery.

When temporal incidence of appendage injury was compared with the opening and closing of the commerical Dungeness crab fishing season, considerable appendage injury occurred when the fishery was closed. Closure of the fishery traditionally occurs during the crabs' mating period, when a high percentage of soft-shelled female crabs are present in the population. There was, however, some overlap in late July and early August in fishing, molting, and mating. Excluding damage by humans, potential causes of appendage injury are aggression between males competing for females, the cheliped-to-cheliped mating embrace of Dungeness crabs that can last up to a week, cannibalism, and the increased vulnerability of females which molt prior to mating (Butler 1960; Durkin et al. 1984). Damage to Dungeness crabs can also result from other fishing gear such as trawls (Reilly 1983), but no other commercial fisheries occurred in the study area while the Dungeness crab fishery was closed.

The results of our studies indicate that Dungeness crabs in southeastern Alaska are in comparable condition to adult populations of Dungeness crabs examined in Washington and Oregon, in terms of appendage injury. Further studies are needed to investigate the effect of appendage injury on survival of Dungeness crabs and the contribution of handling injury and mortality of crabs in the commercial fishery.

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SUSAN M. SHIRLEY
THOMAS C. SHIRLEY

Juneau Center for Fisheries and Ocean Sciences
University of Alaska–Fairbanks
11120 Glacier Highway
Juneau, AK 99801

REEXAMINATION OF THE USE OF OTOLITH NUCLEAR DIMENSIONS TO IDENTIFY JUVENILE ANADROMOUS AND NONANADROMOUS RAINBOW TROUT, *SALMO GAIRDNERI*[1]

Otoliths are a potential source of taxonomic characteristics for identifying stocks of fish (Ihssen et al. 1981). Differences in dimensions of the otolith nucleus have provided a basis for separating winter from summer races of steelhead, anadromous rainbow trout, *Salmo gairdneri*. In addition, otoliths provided data from which to distinguish steelhead from resident nonanadromous forms as well (McKern et al. 1974; Rybock et al. 1975). Neilson et al. (1985) studied the development of sagittal otoliths in resident rainbow trout and steelhead from south-central British Columbia, and identified sources of variability in the size of otolith nuclei. However, they were unable to find morphometric differences between the two forms of trout. They concluded that the usefulness of dimensions of the otolith nucleus for separating steelhead from resident rainbow trout was much more limited than that suggested by Rybock et al. (1975) for rainbow trout in the Deschutes River, Oregon.

The difference in mean length of the otolith nuclei between the rainbow trout studied by Rybock et al. (1975) and those studied by Neilson et al. (1985) suggested either population differences or differences in defining the nuclear boundary. These disparate results, which led to opposite conclusions, limit the usefulness of measurements of otolith nuclei for the racial identification of juvenile rainbow trout until the source of these differences is better understood. Consequently, to determine whether juveniles of the two forms could be distinguished by differences in dimensions of otolith nuclei, we measured the nuclei in sagittae from steelhead and resident rainbow trout collected from the same Deschutes River, OR, locations used by Rybock et al. (1975). We used the definitions proposed by Rybock et al. and by Neilson et al. (1985), and compared our measurements for the two forms with each other and with published values.

Methods

Resident rainbow trout and steelhead were col-

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lected from three locations in the Deschutes River, OR. Resident rainbow trout, which were collected from the main stem near the mouth of Nena Creek in March 1985, were mature and smaller (280–450 mm FL) than the steelhead, and, based on analyses of scales and otoliths (McKern et al. 1974), had never entered saltwater. Juvenile progeny of steelhead were collected from Round Butte Hatchery on the Deschutes River in 1984. Wild juvenile rainbow trout (<200 mm FL) of unknown parental origin were collected in 1984 and 1985 from Bakeoven Creek, an important spawning tributary for steelhead in the Deschutes River.

Sagittae removed from rainbow trout were stored in 90% ethanol for up to two months. Before they were viewed, one otolith from each pair was mounted (concave face up) with epoxy on a glass slide. The back of the slide was blackened with indelible ink. The otolith was ground by hand with 600 grit wet sandpaper and periodically inspected under a light microscope at 100× until the microstructure of the nucleus, as described by Neilson et al. (1985), was visible. The otolith was rinsed with 5% HCl for several seconds to remove scratches and improve resolution.

To reduce bias, we coded each slide with a random number and ordered the slides sequentially for viewing. Otoliths were examined with a Zeiss[2] dissecting microscope at 125×. A camera lucida attachment enabled us to use a computer digitizer to measure three dimensions of the otolith. In measuring length and width of the central nucleus, we used the first growth increment encircling all the central primordia, which was the nuclear boundary defined by Neilson et al. (1985). In addition, we measured the maximum length along the longest axis through an area defined by the first metamorphic check, a narrow hyaline ring surrounding an opaque ring with a hyaline center, to replicate the measurements of Rybock et al. (1975).

We used analysis of variance (ANOVA) to test for significant differences in each dimension of the otolith nuclei among groups in our study. Where adequate data were available, we tested for significant differences between groups in our study and similar groups described by Rybock et al. (1975) and Neilson et al. (1985) for mean dimensions of otolith nuclei. Neilson et al. (1985) showed that the mean length of otolith nuclei for rainbow trout incubated at 6.5°C was significantly less than those for trout incubated at 9.5° or 15.0°C. Because of this discrepancy, we evaluated the potentially confounding effects of incubation temperature on the comparisons of otolith dimensions between our samples and those of Rybock et al. (1975), by testing the hypothesis that water temperatures during 1967–69 were higher than those during 1982–83. We used a paired t-test of average daily water temperatures recorded by the U.S. Geological Survey on the 1st and 15th day of each month from 1 January to 1 August during 1967–69 and 1982–83 (U.S. Department of the Interior Geological Survey 1967, 1968, 1969, 1982, 1983). These dates represent the incubation periods for most of the resident rainbow and steelhead trout sampled in our study and by Rybock et al. (1975). Incubation temperature for steelhead at Round Butte Hatchery is from hatchery records. We estimated spawning and incubation periods for resident rainbow and steelhead trout on the basis of reports of the Oregon Department of Fish and Wildlife (Fessler 1972) and personal observations.

Results

For each dimension, we failed to reject the hypothesis ($\alpha = 0.05$) that rainbow trout collected from different populations for our study had otolith nuclei of the same size (Table 1). Therefore, we concluded that these dimensions could not be used to discriminate between the resident and steelhead forms of rainbow trout sampled in our study.

Water temperatures during 1967–69 were slightly greater than those during 1982–83 ($t = 2.03$, df = 14, $P = 0.03$). Mean difference between the two periods was 0.8°C. Spawning dates for resident rainbow trout and steelhead differ; steelhead spawn from January to April and resi-

TABLE 1.—Means, standard errors (in parentheses), and sample size for three otolith dimensions in resident rainbow trout and steelhead from three Deschutes River populations.

Populations compared	No. of fish	Dimensions of nuclei: Nucleus length (mm)	Nucleus width (mm)	Check length (mm)
Resident rainbow trout	44	0.173 (0.006)	0.070 (0.003)	0.323 (0.012)
Hatchery steelhead	30	0.190 (0.006)	0.070 (0.002)	0.349 (0.009)
Suspected wild steelhead	32	0.178 (0.006)	0.069 (0.002)	0.312 (0.007)

[2]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

dent rainbow trout spawn from May to mid-July (Fessler 1972). Mean water temperature during the period of steelhead egg incubation was 8.4°C for 1967–69 and 7.6°C for 1982–83. Mean water temperature during the period when resident rainbow trout eggs were incubating in the main stem of the river was 12.6°C in 1967–69 and 11.9°C in 1982–83. Incubation temperature for steelhead at Round Butte Hatchery was 10°C and did not vary.

The dimensions of otolith nuclei from resident rainbow trout and steelhead in our study were indistinguishable from those in fish from British Columbia. No significant difference ($\alpha = 0.05$) in mean length of otolith nuclei existed between the British Columbia steelhead incubated at 9.5° or 15°C and suspected wild steelhead from Bakeoven Creek or Round Butte Hatchery steelhead incubated at 10°C. Among resident rainbow trout, the mean length of otolith nuclei for fish from the Deschutes River was also not significantly different from that for fish from British Columbia incubated at 9.5° or 15°C. Because Rybock et al. (1975) did not provide variances, we were unable to test the hypothesis that means from our study coincided with theirs. However, mean length and width of otolith nuclei in our study were 29 and 55% less, respectively, for resident rainbow trout and 49–70% less, respectively, for steelhead than those studied by Rybock et al. (1975).

Discussion

The similarity of our results to those of Neilson et al. (1985), who used similar methods, might be expected for different populations under similar genetic and environmental control. The disparate results of our study and that of Rybock et al. (1975) for the same populations after little genetic change (based on comparisons of unpublished, biochemical genetic data for these populations from 1972 to 1974 and 1984 to 1986) and little environmental change partly reflected the use of different definitions for the nucleus. We defined the nuclear boundary as the first growth ring surrounding all the fused primordia, whereas Rybock et al. (1975) defined the nucleus as the hyaline area in the center of the otolith that is bounded by a metamorphic check formed at hatching; they resolved the check by rendering the otolith with HCl. We also measured the length of the check surrounding the nucleus, as-defined by Rybock et al. (1975), which we found either to correspond with the area enclosed by the first check or to increase in density of growth increments surrounding both the central and rostral primordia. The close similarity between our estimate for Round Butte Hatchery steelhead (0.349 mm) and the mean calculated by Rybock et al. (1975) for steelhead (0.354 mm) suggested similar checks. It is unclear, however, why values for resident rainbow trout for this dimension and the results of tests to discriminate races differed between the two studies. Rybock (1973) noted that the nuclear check could not be distinguished in 29% of the otoliths and that the use of HCl may have caused the frequent confusion between the metamorphic check and other groups of daily growth rings. The grinding and polishing of otoliths greatly reduce this source of error. Neilson et al. (1985) also discouraged the use of metamorphic checks as boundaries because the causal links between checks and developmental events, such as hatching, have not yet been established.

Neilson et al. (1985) demonstrated that nuclear length increased significantly with increase in incubation temperature from 6.5° to 9.5°C but not from 9.5° to 15°C. Although average water temperatures in the Deschutes River were 0.8°C lower during 1982–83 than in 1967–69, it is unlikely that such differences completely explain the greater estimates of mean length and width of otolith nuclei in the earlier study by Rybock et al. (1975). Rybock et al. (1975) calculated mean nuclear lengths and widths of 0.354 and 0.230 mm for steelhead and 0.243 and 0.154 mm for resident rainbow trout in the Deschutes River. Our estimates were 29–70% less than their estimates for a 0.8°C difference; whereas under controlled conditions in British Columbia, mean nuclear length for resident rainbow trout at 6.5°C was 18% less for resident rainbow trout and 21% less for steelhead than the nuclear length for fish incubated at 9.5°C, a difference of 3°C (Neilson et al. 1985).

Comparisons of otolith nuclear dimensions between resident rainbow trout and steelhead incubated at similar temperatures would establish whether significant differences exist for these measurements between the two races from the Deschutes River. The use of a common definition of nuclear boundaries would allow better comparisons between studies. However, given the disparate results of our study, which were similar to the results of Neilson et al. (1985), and the original study for steelhead and resident rainbow trout in the Deschutes River, as well as our failure to discriminate between races using both nuclear definitions proposed by Neilson et al. (1985)

and Rybock et al. (1975), we believe that population differences do not explain the differences in results between the studies of Rybock et al. (1975) and Neilson et al. (1985). Furthermore, our study provided strong evidence to support the conclusion of Neilson et al. (1985) that the usefulness of measurements of otolith nuclei to identify sympatric juvenile progeny of resident rainbow trout and steelhead reared in the wild may be limited.

Acknowledgments

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KENNETH P. CURRENS
CARL B. SCHRECK
HIRAM W. LI

Oregon Cooperative Fishery Research Unit
Oregon State University
Corvallis, OR 97331[3]

[3]Cooperators are Oregon State University, Oregon Department of Fish and Wildlife, and U.S. Fish and Wildlife Service.

AGE-SPECIFIC VULNERABILITY OF PACIFIC SARDINE, *SARDINOPS SAGAX*, LARVAE TO PREDATION BY NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

To a large degree interannual variability in recruitment determines the size of pelagic fish populations. Recruitment to the Pacific sardine, *Sardinops sagax*, population off California varies from year to year over several orders of magnitude and is unrelated to spawning stock size (Murphy 1966; MacCall 1979). Variable mortality rates in the first year of life must determine year-class strength, although the sources of this variability are unknown. Mortality rates in the earliest stages are size specific with highest rates in the egg and yolk-sac stage (Ahlstrom 1954; Butler 1987) and may contribute to variability in year-class strength (Smith 1985).

The sources of mortality of sardine larvae have yet to be investigated. In other pelagic larvae, mortality is due to either starvation or predation, and starvation is significant only during the brief period after the onset of feeding (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986; Owen et al. 1987). In sardines, significant mortality occurs during the egg and yolk-sac stages (Ahlstrom 1954) and this mortality can only be due to predation. Variable mortality in older larval and juvenile sardines may also contribute to variability in recruitment, and this mortality, as in other fishes, may also be due to predation (Hunter 1984).

The objective of this paper was to determine the size-specific vulnerability of Pacfiic sardine larvae to predation by adult northern anchovies, *Engraulis mordax*. The vulnerability of cape anchovy and northern anchovy larvae to

cannibalism has been investigated by Brownell (1985) and Folkvord and Hunter (1986) and found to be an important source of mortality. In this paper the vulnerability of sardine larvae will be compared with that of anchovy larvae and differences in the biology of sardines and anchovies will be discussed.

Our approach was to observe the avoidance behavior of Pacific sardine larvae in response to predatory attacks by northern anchovy adults. Adult northern anchovy were chosen as a predator because the northern anchovy was the most abundant pelagic fish in the California Current region during the waning years of the sardine fishery and because its planktivorous diet includes fish eggs and larvae (Loukashkin 1970; Hunter and Kimbrell 1980).

Materials and Methods

Experimental Fishes

The Pacific sardine larvae used in the experiments were reared from eggs spawned in the laboratory. Adult Pacific sardines were collected off San Diego and held in 175 m^3 aquarium for six months. Males and females with developing gonads were isolated in spawning tanks and injected with 250 mg human chorionic gonadotropin and on the following day injected with 200 units pregnant mare serum and 20 mg salmon pituitary extract. On the third day fertilized eggs were collected from the spawning tank. Larval rearing procedures follow those described by Hunter (1976). Temperature in the rearing tanks was maintained at 21°C.

Apparatus and Procedures

Experimental apparatus and procedures were the same as those described by Folkvord and Hunter (1986) but will be briefly outlined here. Experimental predators were two groups of 5 adult northern anchovy (range of standard lengths 8.4–9.2 cm). Predators were maintained in two rectangular fiberglass tanks ($0.75 \times 2.15 \times 0.83$ m = 1.35 m^3) and fed adult brine shrimp except on days of experimental observation. Seawater was supplied continuously to the tanks except during experiments. The temperature in the observation tank ranged from 16.2° to 22.8°C (mean = 20.1°C). Two 100 W incandescent lamps produced 2,000–3,000 mc at the surface of each tank. A black plastic tent enclosing a window on one side of the tank provided a darkened observation chamber.

Each trial consisted of the encounter of three prey with the predators. Prey were introduced into the observation tank with a clear glass beaker. Initial feeding behavior of the predators is quite variable but becomes less variable as the predators become accustomed to prey in the tank. For this reason, prior to each experiment adult *Artemia* were introduced as prey for five consecutive trials to standardize predator behavior. After the preliminary trials with *Artemia*, three trials with sardine larvae were alternated with one trial with brine shrimp until 18 trials with sardine larvae were completed. Each experiment was concluded with a trial of brine shrimp to test for satiation.

The number of observations for each larval size class was the total number of predator-prey interactions observed among larvae in that size class. The mean standard length was determined from 20 larvae sampled randomly from the rearing tank on the day of each behavior experiment. The numbers of observations for each size class (mean SL) were 8.0 mm, 41; 11.3 mm, 51; 12.1 mm, 114; 12.7 mm, 46; 14.1 mm, 81; 17.6 mm, 104; and 19.6 mm, 69. Experiments were not extended to larger sizes due to insufficient numbers of larvae.

Classification of Behavior

Prey behavior was scored only when the predator attacked a prey. Four measures of predator-prey interactions were calculated: predator attack distance, the distance from which the predator responded to the prey and initiated its attack; frequency of avoidance response; frequency of escapes; and predation rate (percentage of larvae captured during the 5-min trials). An avoidance response was a change in speed or trajectory of a larvae before the predator had completed its attack by closing its mouth. An escape was defined as a larval response in which the predator failed to capture the larvae in a single attack. Typically adult anchovy make a single attack on a prey item and do not pursue a prey that escapes (Folkvord and Hunter 1986) but rather continue searching the tank. Thus attacks on one prey item were recorded twice if the first attack was unsuccessful. Although predator attack distance was recorded, this measurement is highly subjective and comparison with the measurements of other observers is suspect. We did not analyze predator attack distance for this reason.

To compare response and escape behaviors of Pacific sardine with those reported by Folkvord and Hunter (1986) for northern anchovy at similar stages of development, mean lengths were converted to ages using field growth rates back-calculated from otolith increment widths for each species. Confidence limits of the percentage of larvae responding or escaping attack were estimated assuming the binomial distribution.

Results

Probability of Response to Attack

The youngest larval stages of both sardine and anchovy were the most vulnerable to predation. Only 17% of 8 mm sardine larvae (smallest size tested) responded to attack by adult anchovy. With increasing size more sardine larvae responded to attack. At 20 mm, the largest size tested, 61% of the larvae responded to attack. The response rate of Pacific sardine larvae was consistently lower than that of northern anchovy larvae of similar lengths (Fig. 1). Although this difference in responsiveness could be due to differences in the observer, it may also be explained by the difference in age of anchovy and sardine at the same length. Sardine larvae are about 6.2 mm when they begin feeding (age = 5 days from fertilization at 17°C), whereas first-feeding anchovy larvae are only about 4.3 mm (age = 5 days from fertilization at 17°C) (Zweifel and Lasker 1976). Sardine larvae also grow faster than anchovy larvae at the same temperature (Butler and Rojas de Mendiola 1985). Thus, sardine larvae are younger at a given size than anchovy larvae.

Since the latency of response to attack must be related to the development of the central nervous system (Webb 1981; Webb and Corolla 1981), it may be more appropriate to compare sardine larvae with anchovy larvae of the same age. For that reason lengths of the larvae of both species were converted to age using growth rates measured in the field (Methot and Kramer 1979; Butler 1987). Comparison of the percentage of larvae responding to attack at a given age (Fig. 2) reveals no significant difference in the rate of development of response to attack. Thus, the escape response develops at the same rate in Pacific sardine and northern anchovy, and the difference in proportion of larvae responding at a given size (Fig. 1) is due to the difference of size at hatching and the difference in growth rates of the two species.

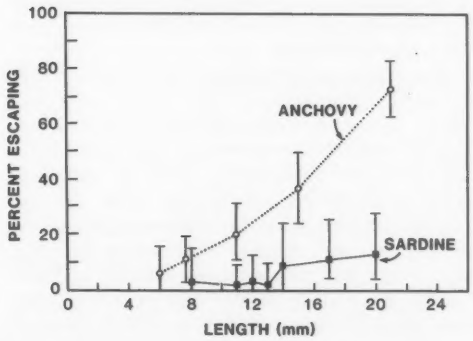

FIGURE 1.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

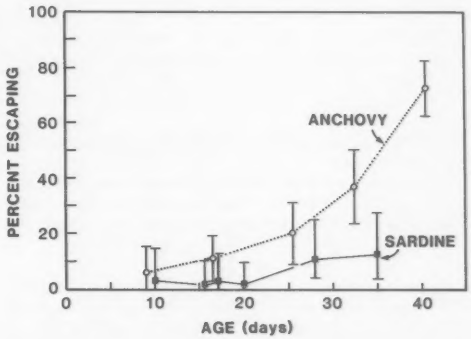

FIGURE 2.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

Probability of Escaping Attack

The ability to successfully avoid attack increased with size of Pacific sardine as well as northern anchovy. Few small larvae of either specie escaped attack by adult northern anchovy. Only 3% of 8 mm sardine larvae escaped attack and the percentage of larvae escaping increased to only 11% for 17 mm larvae and 13% for 20 mm

larvae (Fig. 3). The proportion of small anchovy larvae escaping attack was also low (6%) but increased with size to 73% of 22 mm larvae (Folkvord and Hunter 1986). The numbers of larvae escaping attack were significantly different between anchovy and sardines at sizes larger than about 13 mm. Conversion of lengths to age using field growth rates does not eliminate the differences between sardine and anchovy (Fig. 4). Sardine larvae older than 20 days were more vulnerable to predation than anchovy larvae of the same age (Fig. 4).

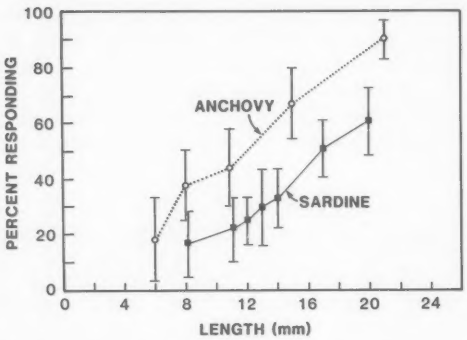

FIGURE 3.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

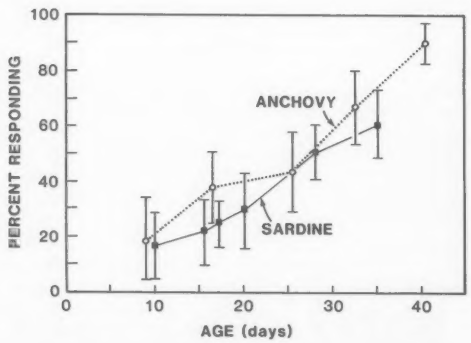

FIGURE 4.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

Discussion

The proportion of Pacific sardine larvae responding to attack and escaping attack increased with size and with age. Our results differ from those reported by Folkvord and Hunter (1986) for anchovy larvae in the rate at which sardine larvae respond and escape attacks at given sizes and ages. It should be noted that, although the methodology was the same, the observers were different. This difference could affect rate of response to attack. It also should be noted that the size of adult anchovy used by Folkvord and Hunter (1986) ranged from 83 to 89 mm SL, whereas the size range was 84–95 mm SL in our study and that the size of predator influences the number of larvae escaping (Folkvord and Hunter 1986). The slightly larger size of predators used in this study is not sufficient to explain difference in escapement, nor is the difference in observer likely to affect the rate of escapement since the observer's task is to examine whether the larvae are escaping or are being eaten.

The greater vulnerability to predation of sardine larvae than anchovy larvae has interesting implications. In general, larger larvae are less vulnerable to predation than small larvae. Bailey (1984) and Bailey and Batty (1983) compared the vulnerability of cod, flounder, plaice, and herring larvae to predation by invertebrate predators. They found that herring larvae were the least vulnerable larvae because herring were more reactive and had the greatest escape speeds. Sardine larvae are larger at hatching and at a given age are larger than anchovy larvae. In our experiment sardine larvae react to predatory attacks at similar rates as anchovy larvae, but escape attack at a much lower rate.

This difference in vulnerability to attack may be due to differences in swimming behavior. Anchovy larvae swim using beat and glide locomotion (Hunter 1972). The escape behavior is usually a burst of swimming from a motionless position (Folkvord and Hunter 1986). We observed that sardine larvae, however, swim continuously and they respond to attack by changing direction and increasing speed. This difference in swimming mode may affect escape behavior in two ways. The escape behavior of sardine larvae may be less flexible than that of anchovy larvae because the direction the sardine larvae takes is largely determined by its trajectory. Since sardine larvae cruise, their scope for activity (escape behavior) may be limited. Anchovy larvae accel-

erate from a standing start and have the possibility of moving in a number of directions. We speculate that the beat and glide behavior of anchovy larvae may not only be hydrodynamically more efficient (Weihs 1974) but also may reduce the vulnerability to predation.

Acknowledgments

Roderick Leong maintained sardines in the laboratory and spawned the adults after manipulation with hormones. Sandor Kaupp reared sardine larvae in the laboratory. Arild Folkvord and Clelia Booman elaborated experimental procedures. John R. Hunter commented on the manuscript.

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JOHN L. BUTLER
DARLENE PICKETT

Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, CA 92117

INDUCTION OF SPAWNING IN THE WEAKFISH, *CYNOSCION REGALIS*

Reproductive activity in the weakfish, *Cynoscion regalis*, is associated with extensive, north-south migrations that result in spawning in the estuaries of the Middle Atlantic Bight during the late spring and early summer. Spawning is apparently related to increasing water temperature and day length, but there have been no experimental investigations of specific factors that control this process in the weakfish. In contrast, general aspects of the reproductive biology of the species are well known (reviewed by Mercer 1983). Both males and females become sexually mature at 1 year of age, and remain sexually active throughout their lifespan (10^+ years). Spawning involves external fertilization of eggs by pairs or small aggregations of fish.

There has been limited study of larval development in the laboratory, and descriptions of growth and development of larval weakfish come entirely from field investigations (Lippson and Moran 1974). Weakfish larvae resulting from gametes stripped from sexually mature adults captured in the field have been reared for a few days on natural zooplankton diets (Public Service Electric and Gas Company 1984), but no information is available on mortality or growth rates on prescribed diets and rations. In contrast, Houde and Taniguchi (1981) and Taniguchi (1981, 1982) have conducted extensive investigations of the effects of diet, ration, and temperature on growth and survival of larval spotted seatrout, *Cynoscion nebulosus*, under laboratory conditions. Similar studies have been conducted with other sciaenids including red drum, *Sciaenops ocellatus* (Holt and Arnold 1983; Holt et al. 1981), spot, *Leiostomus xanthurus* (Powell and Gordy 1980), and bairdiella, *Bairdiella icistia* (May 1974).

The present paper describes a technique for induction of spawning in a laboratory population of weakfish and provides preliminary information on early development and growth of weakfish larvae.

Methods

Sixteen adult weakfish, *C. regalis*, (approximately 30–45 cm and 0.5–1.5 kg) were captured in September 1984 in Delaware Bay by hook-and-line. Five of these fish were dissected and found to have regressed gonads. The remaining 11 fish were placed in two large tanks (2,000 L) connected to a 20,000 L recirculating system that delivered temperature-controlled seawater to each tank at 10 L/minute. Water in the recirculating system was replaced approximately monthly. Ordinary white room light was provided by two 1.25 m fluorescent lamps positioned 1 m above the surface of the water in each tank. Initial conditions in the tank were similar to ambient conditions in Delaware Bay in September: 18°–19°C, 30‰, and 12 hours light:12 hours dark. Temperature and salinity in the tanks were measured daily and pH approximately weekly. The pH was maintained between 7.0 and 7.6 by additions of new seawater to the system; this was accomplished by replacing 40% of the water in the system with new seawater approximately monthly.

Fish began to feed 5–7 days after capture. Diet consisted of an ad libitum ration of sliced squid with weekly additions of penaeid shrimp or fresh calf liver. After approximately one month in the laboratory, the fish were subjected to a prescribed regimen of temperature and photophase (Fig. 1). Temperatures were lowered and light phase shortened over a period of three weeks until conditions reached 8 hours light, 13°–14°C; this approximated winter conditions on the continental shelf off Cape Hatteras where adult fish are known to overwinter (Merriner 1976). Fish were held under these conditions for 11 weeks after which temperature was gradually raised and light phase increased until spring conditions of 14 hours light and 22°–23°C were reached. Fish were held at these conditions throughout a period of extended spawning activity. After spawning activity ceased, six newly captured fish were placed in the system to replace fish that had died during the previous year, and the process of gradually changing temperature and photoperiod to winter conditions was repeated (Fig. 1).

Fertilized eggs were buoyant and exited the tanks at the surface via stand pipes that emptied into a sump tank. The drain was located at the bottom of the sump tank allowing eggs to accumulate at the water surface. The presence or absence of eggs in the sump was determined daily with a fine-meshed dip net. After collection, eggs from each spawning were allowed to hatch in 20 L plastic aquaria filled with 5.0 μm filtered seawater at 30‰ and 23°C. Eggs exposed to gentle aeration under these conditions hatched in 24–36 hours.

Larvae were cultured in 2 L beakers filled with filtered seawater (25°C, 30‰, and 5 mg/liter

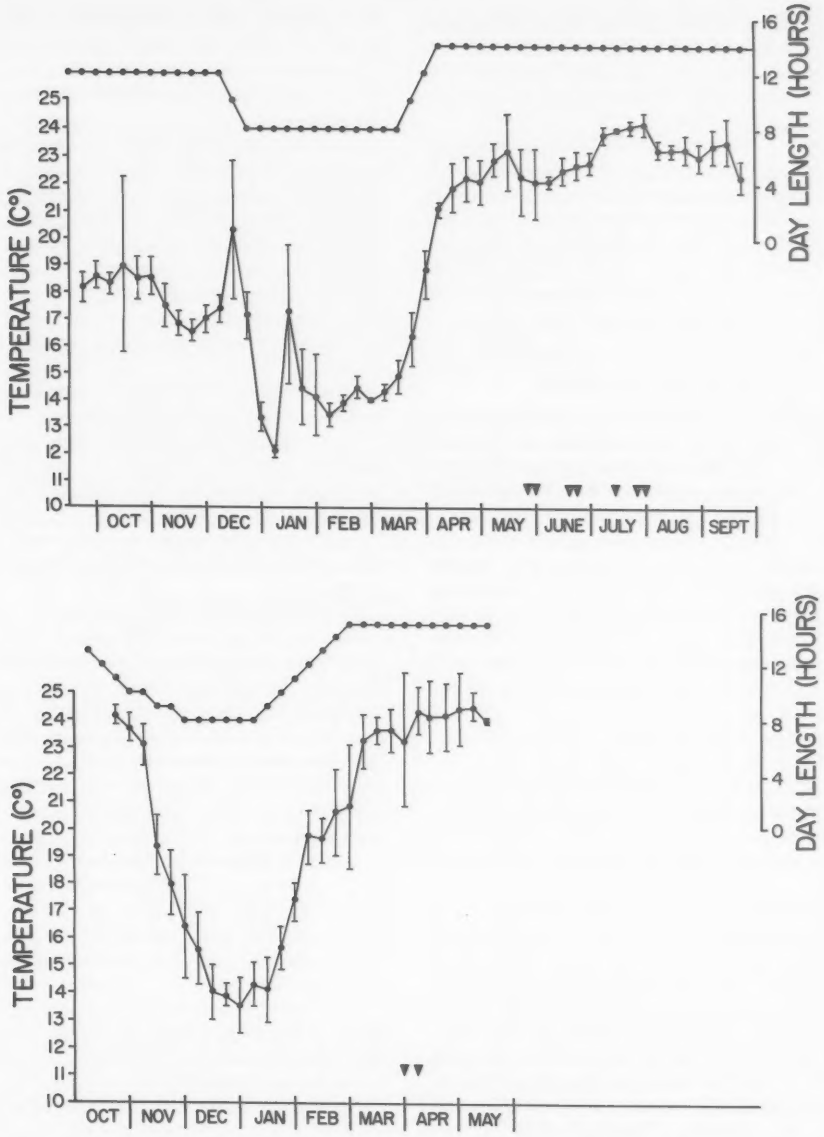

FIGURE 1.—Temperature-photophase regime used to condition northern weakfish, *Cynoscion regalis*, to spawn in the laboratory. Values are 7-d means. Standard deviations are plotted for temperature. Arrows on time axis indicate dates of spawning. A = 1984–85. B = 1985–1986.

chloramphenicol) at a density of 25 larvae/liter. Larvae were fed rotifers, *Brachionis plicatilis*, beginning two days after hatching; on the seventh day after hatching, brine shrimp *Artemia* sp. were added to the diet.

Early larval development from spawning to first feeding was determined for larvae from three separate spawnings. Newly hatched larvae (6–15 hours old) were pipetted into an aquarium and 10–15 removed immediately and preserved in 70% ethanol. Additional larvae were sacrificed daily for nine days. These samples were examined to relate early development and age.

Results and Discussion

Three adult fish died of undermined causes during the period of winter conditions in 1984–85. Four additional fish died after jumping from the tanks. The initial spawning by the remaining population of four fish occurred five weeks after spring conditions were achieved. This was followed the next day by another spawning. Spawning continued for nine weeks at 10–14 d intervals. Spawning episodes usually consisted of production of fertilized eggs over 2 successive days. While actual spawning was never observed, it always occurred between sunset and 08:00 the following day.

After cessation of spawning, the four fish were removed from the tanks and their sex determined. Two of the fish drummed when handled and were clearly males. At least one (and probably both) of the two remaining fish were females. The fish were returned to the system after examination.

The temporal sequence of the spawning events (two successive days at 10–14 d intervals) suggests that each female may have spawned as many as four times during the 9-wk period. This is in contrast to reports for natural populations of *C. regalis* (e.g., Merriner 1976), but has been reported for laboratory populations of other sciaenid fishes. For example, Arnold (1984) observed 82 spawning events in a laboratory population of 12 *C. nebulosus* over a 27-mo period and 52 spawning events in a similar population of six *S. ocellatus* over a 3-mo period. It is not clear why the *C. regalis* in our investigation ceased spawning after several months of long days and high temperatures while the *C. nebulosus* in Arnold's system continued to spawn over a much longer period. Perhaps this is related to the smaller annual variation in photophase and temperature typical of *C. nebulosus* habitats. However, gonadal resorption has been reported for at least one other sciaenid species (*B. icistia*) held in the laboratory for extended periods of long day-length (May 1974).

Spawning from the 1985–86 conditioning period first occurred four weeks after spring conditions were reached with a second spawning nine days later. Further spawning in the 1985–86 population did not occur because of an unidentified infection resulting in the death of all 10 fish in the system over a period of a few weeks. Autopsies revealed that all fish had highly developed ovaries or testes at the time of death.

Newly hatched larvae (6–15 hours old) had a yolk sac, no mouth, and little development of the eyes. By 24–36 hours after hatching, the yolk sac had been virtually absorbed, the mouth was just beginning to form, and the eyes were not yet pigmented. By 48–60 hours, larvae had a completely formed mouth and digestive system, and the eyes were pigmented. Larvae were capable of feeding at this stage.

Chloramphenicol improved larval survival, which was as high as 24% over 11 days. This survival is comparable to that reported for other sciaenid larvae (Holt et al. 1981; Houde and Taniguchi 1981; Holt and Arnold 1983). However, growth was less than the maximum seen in the laboratory for *C. nebulosus*. After 11 days *C. regalis* larvae in the present experiments had grown from a mean, posthatching size of 2.7 mm (36 μg dry weight) to 4.5 mm (235 μg dry weight). In contrast Houde and Taniguchi (1981) found that one group of *C. nebulosus* larvae reached a size of 13.6 mm (7,082 μg dry weight) in 12 days when reared on a concentrated ration of natural zooplankton at very low stocking density and high temperature (32°C). However, when fed a rotifer diet at comparable temperatures and stocking densities, growth of *C. nebulosus* larvae was somewhat less than that of *C. regalis* larvae in the present experiments.

Our results show that the spawning cycle of weakfish can be manipulated to produce repeated spawnings without the aid of hormone injections. While the fish appear to resorb their gonadal tissue after several months of exposure to long day length and high temperature, the differential manipulation of several groups of fish could allow year-round production of fertilized eggs. Furthermore, survival and growth of larvae produced in this manner appear comparable to survival and

growth of other sciaenids reared in the laboratory.

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CHARLES E. EPIFANIO
DAVID GOSHORN
TIMOTHY E. TARGETT

College of Marine Studies
University of Delaware
Lewes, DE 19958

ERRATA

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Botton, Mark L., and John W. Ropes, "Populations of horseshoe crabs, *Limulus polyphemus*, on the northwestern Atlantic continental shelf," p. 809.

Page 809, Table 3, footnote was omitted:

[1]Depth at the end of this tow was 439 m.

Henwood, Tyrrell A., and Warren E. Stuntz, "Analysis of sea turtle captures and mortalities during commercial shrimp trawling," p. 814.

Page 814, paragraph 1, line 3, the equation should read:

E = (nets * length/30.5 m) * (min/60)

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